FIRE-GRAZING INTERACTIONS IN A MIXED GRASS PRAIRIE

A Dissertation

by

JOHN ANDREW HUBBARD

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2003

Major Subject: Rangeland Ecology and Management

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Approved as to style and content by:

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ABSTRACT

Fire-Grazing Interactions in a Mixed Grass Prairie.

(May 2003)

John Andrew Hubbard, B.S.; M.S., University of Arizona

Co-Chairs of Advisory Committee: Dr. Steven R. Archer
Dr. Thomas W. Boutton

Grasslands are characterized by recurring disturbances such as fire and grazing occurring against a background of topoedaphic heterogeneity and climatic variability. The result is a complex, multi-scaled disturbance regime, in which fire and grazing often have interactive roles, yet they have usually been studied independently. Relationships between climate, fire and simulated grazing (=mowing) were explored to determine the roles these disturbances play in shaping patterns and processes in southern mixed grass prairie. A field experiment investigated the potential effects of these disturbances on above and belowground plant productivity, patch dynamics, and soil respiration over a 2-year period characterized by drought (1998) and normal (1999) rainfall.

Spring burning and mowing had interactive effects on aboveground net primary production (ANPP). Consistent with published single factor studies, burning without mowing doubled ANPP, whereas mowing in the absence of burning had neutral effects. However, subsequent mowing on burned plots reduced ANPP gains to levels comparable with all unburned plots. Drought reduced ANPP by 22% relative to a normal rainfall year.

In contrast to the traditional model of root response to defoliation, burning and mowing each stimulated root length recruitment measured with minirhizotrons. However, subsequent mowing on burned plots did not produce additional root recruitment. Fire and mowing appear to interact by affecting different components of root recruitment (production and mortality, respectively). Root biomass recovered from ingrowth cores were not correlated with minirhizotron results, and responded only to drought, suggesting that methodological differences have contributed to the varied root responses reported in the literature.

Drought suppressed soil respiration, diminished soil moisture, and enhanced soil temperature, whereas fire and/or mowing had little effect. Results suggest that any fire or mowing effects on soil respiration in southern mixed grass prairie may be highly constrained by moisture limitations during dry periods.

In summary, patch level response to fire is a pulse of root recruitment followed by increased ANPP, unless subsequent grazing offsets these gains. Grazing alone produces a pulse of root recruitment, perhaps to replace consumed foliage. This study demonstrates the interactive nature of fire and grazing in grasslands, and the perils of single-factor studies.

ACKNOWLEDGEMENTS

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TABLE OF CONTENTS

Page

CHAPTER Page

LIST OF FIGURES

FIGURE Page

FIGURE Page

LIST OF TABLES

CHAPTER I

INTRODUCTION

Ecological drivers of grasslands

While the occurrence of grasses in North America extends to at least the late Cretaceous (70 mya), grasslands seem to be relatively recent phenomena, with fossil evidence dating to the middle Miocene (15 mya), coincident with the uplifts of the Rocky and Sierra Madre Mountain ranges (Van Devender 1995). The broad extent of grasslands sandwiched between the eastern deciduous forests and montane forests of the Rocky Mountains from central Canada to the American southwest (McClaran 1995) appears to be the product of seasonally dry climate (Van Devender 1995). These climatic drivers are evident on a global scale, with grasslands occurring in areas too dry to sustain forests, but with sufficient nutrients and warm-season precipitation to favor grasses over shrubs and true xerophytes (Huston 1994). Nearly a century of ecological research on grasslands (e.g., Aldous 1934, Daubenmire 1968, Anderson 1982, Collins and Gibson 1990, Archer and Smeins 1991, Huston 1994, McPherson 1995, Knapp et al. 1999) has demonstrated the importance of topoedaphic variability and disturbance, particularly fire and grazing, on the development and maintenance of grasslands. Thus, grasslands may be best characterized by recurring disturbances such as fire and

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This dissertation follows the style and format of the journal Ecology.

herbivory (Anderson 1990) occurring against a background of topoedaphic heterogeneity and pronounced climatic variability. The result is a complex, multi-scaled disturbance regime (Collins 1987).

Interaction of disturbances

The most immediate and apparent effect of both fire and grazing is defoliation, which may indicate that these disturbances play an equivalent role in grasslands (Knapp and Seastedt 1986). However, recent research has demonstrated that fire and grazing are not slight variations of the same disturbance mechanism, but have distinct and specific consequences for grasslands (McNaughton 1983, Collins and Uno 1983, Huston 1994, Knapp et al. 1999). Moreover, fire and grazing often interact to drive patch-level structural (Collins and Barber 1985, Collins 1987, Noy-Meir 1995) and functional (Hobbs et al. 1991, Johnson and Matchett 2001) attributes of grasslands. The primary path by which fire and grazing can interact is by affecting the probability of occurrence, intensity, and spatio-temporal scale of each disturbance event. Grazing can reduce fuel loads, and thereby dampen fire intensity, probability of occurrence and spread (Daubenmire 1968). Conversely, burning is well known to attract grazing animals by stimulating the growth of fresh foliage that is relatively palatable and nutrient-rich (Knapp et al. 1999).

Although this interdependence of fire and grazing has been widely observed (Leopold 1924, Campbell 1954, Wright and Klemmedson 1965, Daubenmire 1968, Wright 1969, Norton-Griffiths 1979, Anderson 1982, Madany and West 1983,

McNaughton 1983, Zimmerman and Neuenschwander 1984, Collins and Barber 1985, Collins 1987, Noy-Meir 1995, McNaughton et al. 1998, Knapp et al. 1999), the majority of grassland research studies have treated these disturbances separately (Collins and Gibson 1990, Hobbs et al. 1991). This paucity of investigations of interactive effects has been attributed to the practical limitations and design complexity of implementing factorial field experiments (Collins and Gibson 1990). When fire and grazing have been studied concurrently, the results often strongly diverge from the individual single-factor effects (Collins and Uno 1983, Collins and Barber 1985, Collins 1987, Hobbs et al. 1991, Johnson and Matchett 2001).

This dissertation explores potential interactions between fire and grazing in mixed grass prairie by simultaneously documenting above- and belowground plant production, community dynamics, and soil respiration, moisture and temperature. Chapter II provides an overview of the climate, soils, and vegetation of mixed grass prairie in the Low Rolling Plains of Texas. Details of the experimental design that forms the foundation of this research are also provided in Chapter II. Chapter III explores climate, fire and grazing effects on aboveground net primary production (ANPP) and community dynamics. Fine root response to fire and grazing is documented in Chapter IV, in the context of competing hypotheses of root response to defoliation. Chapter V examines climate, fire and grazing effects on soil respiration, soil temperature, and soil moisture. Results in Chapters III-V are synthesized in Chapter VI. Detailed statistical summaries are provided in Appendix I.

CHAPTER II

STUDY SITE AND EXPERIMENTAL DESIGN

Site description

Research was conducted in the 160-ha Ninemile experimental pasture on the Waggoner Ranch in Wilbarger County, Texas (33° 51'N, 99° 26' W, elevation 381 m). The Ninemile site is typical of the Low Rolling Plains region of Texas, with gentle slopes and extensive flats of honey mesquite (*Prosopis glandulosa* Torr.) savanna and C_3/C_4 mixed grass prairie (Ansley et al. 1998). The distribution and density of honey mesquite in the Low Rolling Plains has increased dramatically during the last century (Ansley and Jacoby 1998, Asner et al. 2003), as has been documented in grasslands throughout the American Southwest (Smeins 1983, Archer 1994). Warm-season shortgrasses and midgrasses and annual forbs dominate mixed grass prairie and herbaceous interstices of mesquite savanna, whereas cool-season midgrasses and annuals are most abundant under mesquite canopies and grassland sites protected from livestock grazing (Ansley and Jacoby 1998).

The Ninemile site contains an approximately equal mixture of cool (C_3) and warm (C_4) season grasses. The dominant C_3 grasses include the native perennial bunchgrasses Texas wintergrass[1] (*Nasella leucotricha* Trin. & Rupr.) and the exotic

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1: Plant nomenclature follows Gould (1975).

annual Japanese brome (*Bromus japonicus* Thunb.). The dominant C_4 grasses include the perennial bunchgrasses sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.) and sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray), and the stoloniferous, sod-forming buffalograss (*Buchloë dactyloides* (Nutt.) Engelm.). Common forbs include silverleaf nightshade (*Solanum elaeagnifoium*) and western ragweed (*Ambrosia psilostachya*). Soils at the Ninemile site are alluvial clay loams classified as fine, mixed, thermic Typic Paleustolls of the Tillman series (Ansley et al. 1990). See Ansley et al. (1990, 1998) and Heitschmidt et al. (1985, 1989), for a more detailed description of the vegetation and soils of the Ninemile site.

Experimental plots were located within portions of the Ninemile Pasture which had not been burned for at least 25 years or grazed for 10 years. The herbaceous composition of this area was ca. 60/40 cool season to warm season grasses, with woody plants almost entirely absent because of root plowing in the early 1970s. Sideoats grama was broadcast seeded on the site immediately following root plowing.

Climate

The Low Rolling Plains region lays along the transition between the mild, semi-arid Continental Steppe of North Texas and the hot Subtropical-Subhumid climate of Central Texas (Larkin and Bomar 1983). The Low Rolling Plains are characterized by dry winters and hot summers, with substantial diurnal temperature extremes and irregularly spaced precipitation events. Mean annual precipitation for the Ninemile site (665 mm) is bimodally distributed, with peaks in May (ca.18%) and September (ca.

12%). Growing season (March – August) precipitation averages 420 mm (National Oceanic and Atmospheric Administration [NOAA] 1999). Mean extremes in air temperatures range from 36^{o}C in July to -2.5^{o}C in January.

This study was conducted in 1998 and 1999. Texas endured droughts in 1996 and 1998, while the El Nino year of 1997 was one of the wettest years in the previous half century (NOAA 1998). The 1998 drought began in March with the abrupt transition from El Nino to La Nina conditions and continued through February 1999 (Texas Water Development Board, 2002). Statewide, April – June of 1998 were the driest months on record, while July was the hottest (NOAA 1999, Texas Water Development Board, 2002). Precipitation at the Ninemile site tracked these regional trends, with 111% normal precipitation in 1997, whereas 1998 and 1999 had 72% and 89% normal precipitation, respectively (Figure 1). Growing season precipitation during the two years of this study (1998 and 1999) was only 24% and 78% of normal. Mean monthly air temperatures were substantially higher than normal during both the 1998 and 1999 growing seasons (Figure 2). Because all experimental plots and treatments were randomly assigned to a treatment year (1998 or 1999), the substantial climatic differences between the drought of 1998 and relatively average conditions of 1999 could be statistically analyzed as a treatment, as described in the experimental design section below.

Experimental design and treatments

In the southern Great Plains, wildfires typically occur during the dry period at the

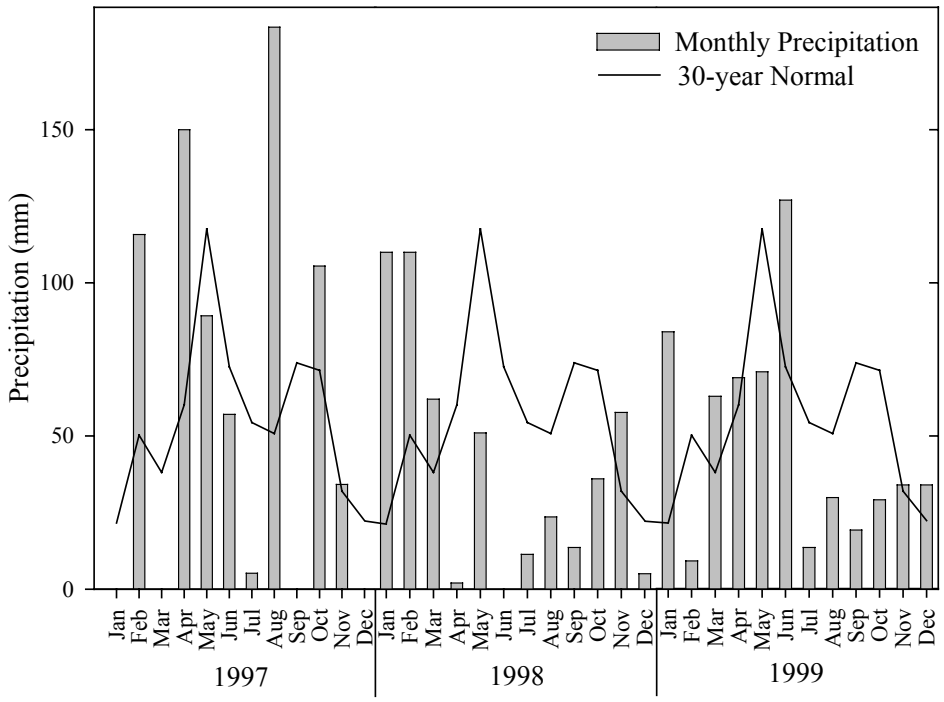

FIG. 1. 1997-1999 monthly (bars) and 30-year normal precipitation (line) at the Ninemile Pasture on the Waggoner Ranch, Wilbarger County, Texas.

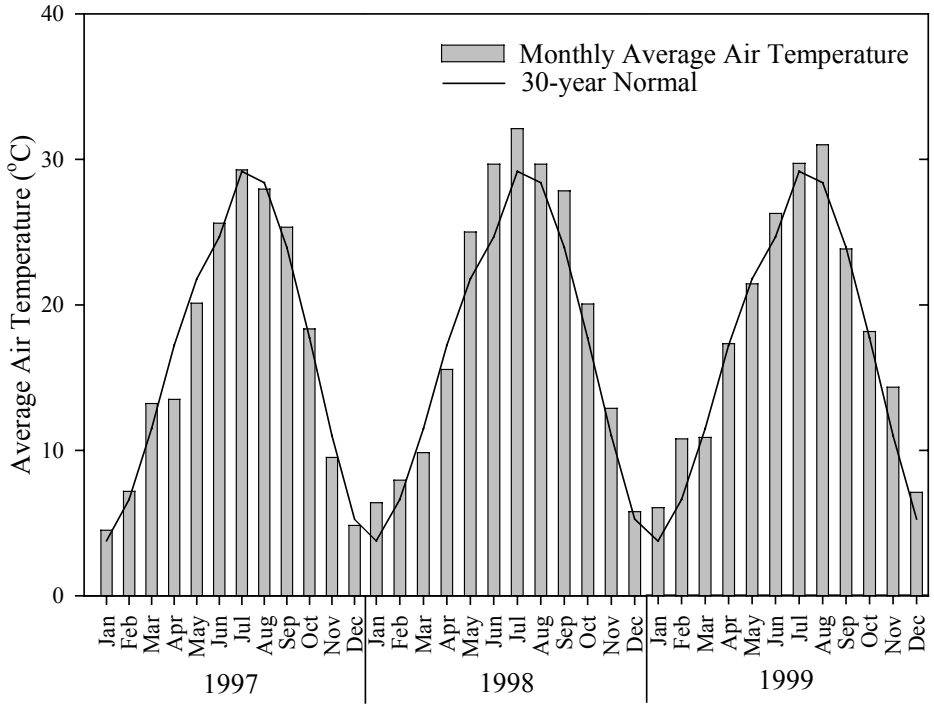

FIG. 2. 1997-1999 monthly average (bars) and 30-year normal air temperature (line) for Vernon, Wilbarger County, Texas.

end of the growing season (August to October; Wright and Bailey 1982). "Cool season" prescribed fires are commonly applied during January through April to impede the growth and reproduction of the winter-deciduous shrub honey mesquite and to stimulate forage production for livestock (Wright and Bailey 1982, Scifres and Hamilton 1993, Ansley et al. 1998). Livestock are typically introduced on these sites approximately six weeks following burning to utilize the relatively nutritious and palatable regrowth (Scifres and Hamilton 1993). For this study, mowing was used to simulate grazing as actual grazing by livestock was not practical. While mowing is an imperfect facsimile of grazing (Biondini et al. 1998), it is a reasonable approximation that has been widely used to simulate grazing in experimental studies (Hobbs et al. 1991, Collins and Steinauer 1998, Collins et al. 1998).

The experimental design was a 3 x 2 factorial involving two levels of prescribed burning [cool season burn (CB), and non-burned controls (NB)] and three levels of simulated grazing [mown once (OM) in late April to 5 cm height (= "light grazing"); mown repeatedly (RM) to maintain 5 cm height (= "heavy continuous grazing"); and non-mowed controls (NM; = "non-grazed")]. Cool season (or "spring") burns were applied in early March of 1998 and late February of 1999, whereas initial mowing treatments were applied in late April of both years. To contrast cool season and warm season burning, a warm-season prescribed fire treatment (WB) was applied to five unmown plots in October of 1998, and monitored as a separate treatment during the 1999 growing season. The autumn burning treatment was not applied in a completely factorial design, as there was insufficient space on the experimental site to add the 15

plots that would be required. The specific dates of cool and warm-season prescribed burns were dictated by climatic conditions. Treatments were assigned randomly to sixty-five 6 x 6 meter plots (n= 5 replicates/treatment combination/year) such that the experiment initiated in 1998 (total = 30 plots) was completely replicated in 1999 (total = 30 plots + five warm season burn plots) on new, randomly-assigned plots (Figure 3).

Cool and warm season burns were imposed using the ring-fire prescribed burn technique (Pyne et al. 1996). Fire characteristics were quantified in each plot (Table 1) by measuring temperatures continuously at 100, 30, and 10 cm above the soil surface, at the soil surface, and at15 cm beneath the mineral soil surface with glass-insulated type K thermocouples (20AWG; 0.8 mm diam.; Omega Engineering, Stamford, CT, USA) connected to a Campbell CR 7 datalogger (Campbell Scientific, Logan, UT, USA) in a fireproof container (Jacoby et al. 1992). Mowing treatments were imposed six weeks following the cool season burn treatment in order to mimic livestock grazing practices typical for this region (Scifries and Hamilton 1993, Ansley et al. 1998). Plots were mowed using a lawn mower; all cut plant material was collected and transported offsite.

Plots were sampled monthly throughout the growing season (ca. March through August) of 1998 and 1999. Each plot was separated into thirty-six 1-m^2 subplots (Figure 4), in a combined split-plot and repeated measures design. Subplots were randomly assigned a particular month during which split-plot response variables (aboveground biomass, soil respiration, soil temperature) were measured. To minimize potentially confounding effects of sampling-related disturbance, split-plot subplots were never re-sampled following the initial data collection. Repeated measures variables

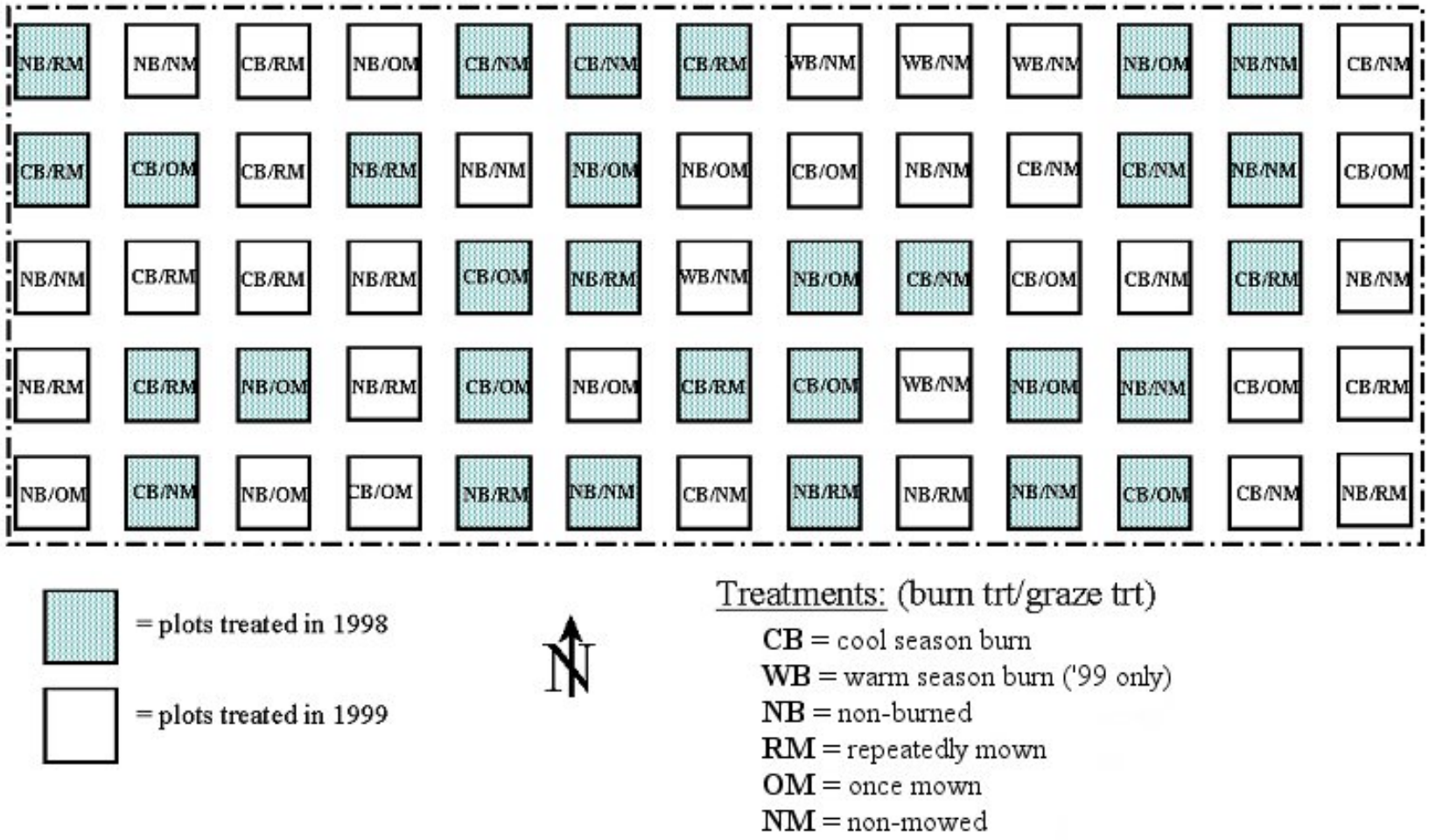

FIG. 3. Arrangement of (6 x 6m) plots for fire X mowing experiment at the Waggoner Ranch Ninemile Pasture, Wilbarger County, Texas.

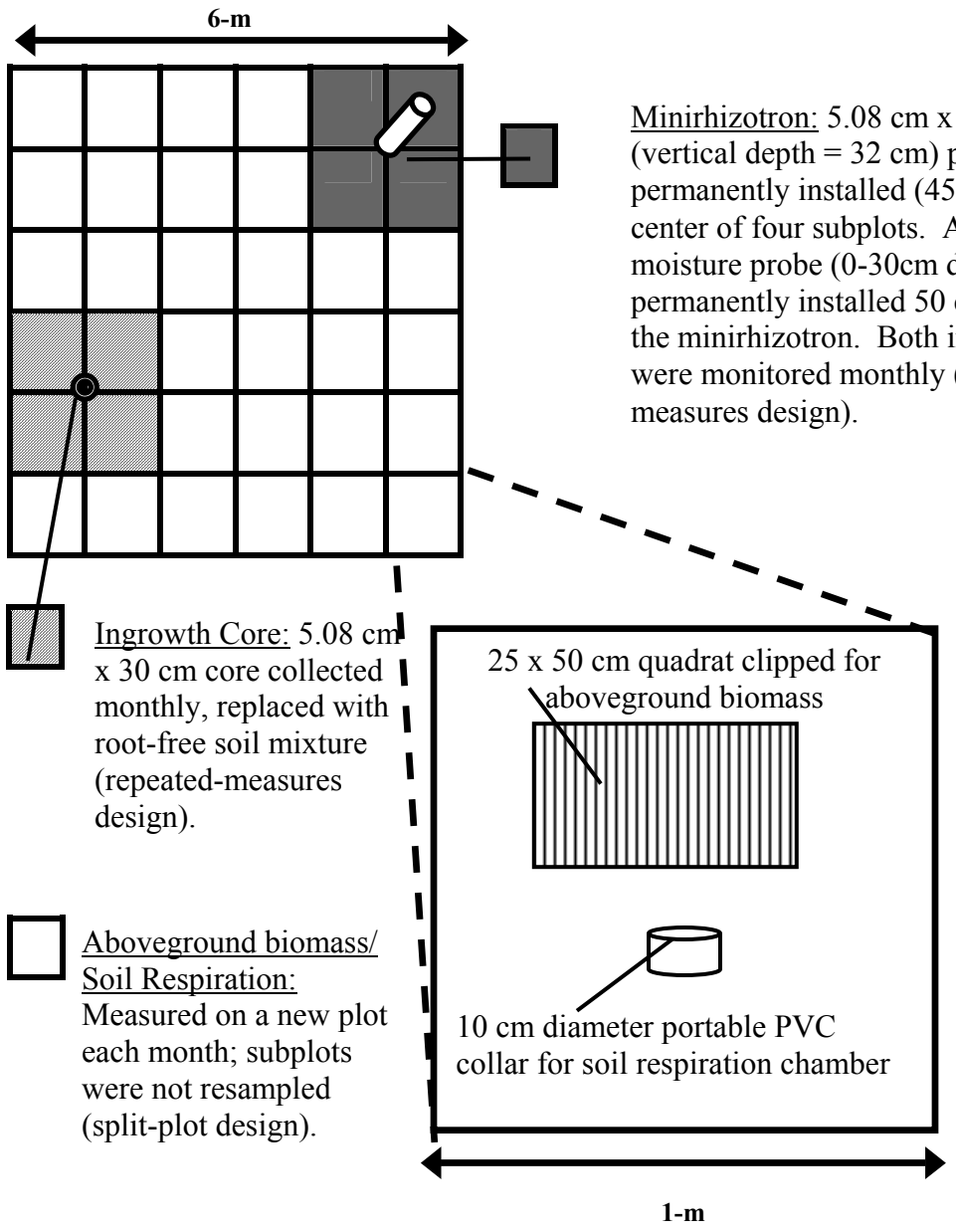

FIG. 4. Sampling design. Each 6 x 6 treatment plot was divided into 1 x 1 m subplots, with four subplots randomly designated for minirhizotron observations and soil moisture probes and four for root ingrowth cores; the remaining 28 subplots were selected at random for monthly aboveground biomass and soil respiration measurements.

(minirhizotron observations, root ingrowth cores, soil moisture) were randomly assigned to permanent subplots within each plot. Multivariate analysis of variance (MANOVA; Sokal and Rohlf 1995, Littell et al. 1992) was used to test hypotheses on repeated measures and split-plot designs. Univariate analysis of variance (ANOVA) for repeated measures designs was not used, as data rarely met Mauch's sphericity criteria, a key assumption for accurate results (Littell et al. 1992). Tests of significance for "within subjects" effects were adjusted to correct for spatial autocorrelation among repeated measures factors (month), providing more conservative tests (Greenhouse and Geisser 1959). In most cases, raw data had to be transformed (Sokal and Rohlf 1995) to approximate normality and heteroscadascity of variances. The particular transformation used (log, square root, arcsine) for each analysis is listed in the MANOVA tables in Appendix I (see Sokal and Rohlf 1995 for a discussion of transformations in parametric statistics). Data presented in figures and tables are back-transformed means. As the repeated measures factor for each MANOVA was the month of the growing season, significant "within subjects" differences can be interpreted as "within season" differences with respect to a given treatment. These within-season effects do not necessarily indicate overall differences through the entire growing season. "Between subjects" results indicate differences (or lack thereof) due to treatment effects that supercede intraseasonal variability. More detailed descriptions of the experimental design and statistical analyses as they pertain to the specific response parameters are provided in the corresponding chapters.

CHAPTER III

EFFECTS OF FIRE AND GRAZING ON ABOVEGROUND NET PRIMARY PRODUCTION AND COMMUNITY DYNAMICS

Introduction

Climate aside, fire and grazing are the primary factors influencing the development and maintenance of grasslands (Anderson 1990). In fact, the occurrence and persistence of most grasslands seem to require the relatively frequent occurrence of these disturbances, often in combination (Huston 1994). Fire and grazing play critical and interactive roles in determining grassland structure (Collins and Barber 1985, Collins 1987, Mark 1994, Noy-Meir 1995) and function (Hobbs et al. 1991, Benning and Seastedt 1997). The fire-grazing interaction is mediated by species life history traits in conjunction with climatic and edaphic factors. The net outcome of these interactions determines the relative competitive ability (and thus community representation) of each species (Collins 1987).

Fire X grazing interactions may have profound effects on patch dynamics of the Low Rolling Plains of Texas. Vegetation of the Low Rolling Plains is comprised of patchily distributed honey mesquite (*Prosopis glandulosa*) thickets and savannas in a matrix of mixed grass prairie (Ansley et al. 1998). Mixed grass prairies of this region are dominated by variable proportions of cool season (C_3 photosynthetic pathway) and warm-season (C_4 photosynthetic pathway) grasses, with extended hot and dry summers

dividing relatively wet and cool spring and autumn seasons (Heitschmidt et al. 1989). Warm season shortgrasses and midgrasses dominate prairie and herbaceous interstices in open areas, whereas cool season midgrasses and annuals are most common under mesquite canopies and on sites protected from livestock grazing (Ansley and Jacoby 1998). The spatial and temporal heterogeneity of C_3 vs. C_4 grasses suggests a dynamic mixture in which dominance and relative abundance of grass species are dictated by disturbance and microclimate. Thus, species composition would be expected to be sensitive to alterations in disturbance regimes and climatic extremes.

One of the defining characteristics of humans has been the ability to acquire resources by innovative manipulation of ecosystems, including the domestication of grazing animals for food and fiber. Prior to the widespread adoption of modern agriculture, the selective application of fire to landscapes was perhaps the most preeminent tool employed (Pyne et al. 1996). This is still the case in the mixed grass prairies of northcentral Texas, prescribed fires are often used to stimulate production of desired grasses for livestock production and retard encroachment of woody plants (Wright and Bailey 1982, Scifries and Hamilton 1993, Ansley and Jacoby 1998). Prescribed fires are typically implemented at the beginning of the growing season, just prior to the onset of spring rains (Scifries and Hamilton 1993), whereas most wildfires occur in conjunction with thunderstorms during hot and relatively dry months of late summer and early fall when fine fuel loads are relatively high (Wright and Bailey 1982). As these two fire regimes occur under dissimilar climatic conditions and on opposite ends of the growth cycle of mixed grass prairie species, the consequences for vegetation

dynamics are often quite different. Prescribed fires during winter/spring months tend to suppress annuals and cool season (C_3) perennial grasses while favoring warm-season species (Daubenmire 1968, Anderson et al. 1970, Bailey and Anderson 1978). By contrast, late summer/fall burning minimizes damage to cool season grasses, and may favor C_3 plants over C_4 grasses, although this has not been substantiated in the Rolling Plains (Wright 1974, Whisenant et al. 1984).

Correspondingly, the responses of grassland structure to pre-Anglo European grazing regimes (e.g., intensive but infrequent grazing of free-roaming bison) vs. more managed grazing regimes (e.g., heavy continuous grazing by fenced-in livestock) are also likely to differ (Archer and Smeins 1991, Frank et al. 1998). Potential interactions between these different fire and grazing regimes as mediated by climate and topoedaphic variability suggest a myriad of possible community responses.

Fire and grazing are important determinants of patch level plant productivity in grasslands (Knapp et al. 1999). In their review and meta analysis of 236 studies of grazing effects on aboveground net primary production (ANPP), Milchunas and Lauenroth (1993) concluded that grazing often has a negative effect on ANPP, although in some instances neutral or positive effects were detected. When positive effects occur, they are typically observed on sites with a long evolutionary history of grazing, and relatively low consumption rates, and are assumed to increase with increasing time between grazing events (Georgiadis et al 1989, Oesterheld and McNaughton 1991, Milchunas and Lauenroth 1993, Turner et al. 1993). The frequency and magnitude of

these positive responses to grazing are unclear (Briske 1993), and are debatable (McNaughton 1993, Painter and Belsky 1993).

By contrast, increased ANPP following burning has been commonly observed in grasslands (e.g., Daubenmire 1968, Hulbert 1969, Anderson et al. 1970, Wright 1974, Bailey and Anderson 1978, Towne and Owensby 1984, Abrams et al. 1986, Anderson 1990, Briggs and Knapp 1995), with the greatest increases occurring on infrequently burned tallgrass prairie (Hulbert and Wilson 1983, Seastedt et al. 1991, Briggs et al. 1994, Blair 1997). This response appears to be due to an improved light environment following combustion of detritus (Knapp and Seastedt 1986, Hulbert 1988), and enhanced nutrient use efficiency (NUE) by the dominant C_4 grasses (Ojima et al. 1994, Briggs and Knapp 1995). This compensates for N-limitation that might otherwise result from volatilization (Seastedt and Ramundo 1990). However, neutral or negative effects on ANPP have been observed on sites where soil water content is the primary resource constraint (Dix 1960, Kucera and Ehrenreich 1962, Trlica and Schuster 1969, White and Currie 1983, Engle and Bultsma 1984, Briggs and Knapp 1995, Blair 1997, Knapp et al. 1998a).

Although ANPP response to fire (Towne and Owensby 1984, Hulbert 1988, Briggs and Knapp 1995) and grazing (Daubenmire 1968, Jeffries 1988, Milchunas and Lauenroth 1993) have often been the primary focus of grassland research (Collins and Gibson 1990), most studies have treated these disturbances as independent factors, despite repeated calls for an approach that accounts for potential fire X grazing interactions (Anderson 1982, Collins and Barber 1985, Collins 1987, Hobbs et al. 1991,

Noy-Meir 1995, Johnson and Matchett 2001). Restricting research to single factor "fire *or* grazing" experiments does not accurately reflect the "fire *and* grazing" reality of most grasslands, and may therefore lead to misleading, out-of-context interpretations and projections (Collins and Gibson 1990).

The purpose of this field experiment was to address this gap in grassland ecology by explicitly testing the interactive effects of fire X grazing on ANPP and community dynamics of mixed grass prairie. The following hypotheses were tested:

1. The main effect of burning (in the absence of grazing) will stimulate ANPP (Hulbert and Wilson 1983, Seastedt et al. 1991, Briggs et al. 1994, Blair 1997) as senescent leaves and litter are removed, increasing nutrient and light availability (Hulbert 1988).
2. The main effect of grazing (in the absence of burning) will have neutral or negative effects on ANPP (Biondini and Mankse 1996, Biondini et al. 1998). Impacts of grazing on ANPP will increasingly negative with increasing within-season grazing frequency.
3. Fire and grazing will interact to affect ANPP. Burning will stimulate ANPP, though subsequent grazing on burned plots will dampen this production as fresh green foliage is removed.
4. Fall burning will favor C_3 grasses and forbs relative to C_4 grasses, whereas spring burning will produce the opposite effect (Daubenmire 1968, Wright 1974). Grazing will favor the relative abundance of warm season

shortgrasses (Heitschmidt et al. 1989) such as buffalograss (*Buchloë dactyloides* (Nutt.) Engelm.).

These hypotheses were tested on a southern mixed grass prairie site that had been protected from fire and grazing since the mid-1980's.

Methods

Chapter II provides a detailed description of the study site, experimental design and treatments.

Aboveground biomass

Aboveground biomass on all plots was estimated monthly from March through August by clipping vegetation within 0.125-m^2 frames centered within subplots in a split-plot design (Figure 4). Clipping for biomass estimation was conducted at the beginning of each sampling period, whereas mowing (=simulated grazing) treatments were implemented at the end of each sampling period. Biomass was sorted by species and separated into live (green) and standing dead (non-green) categories. Standing dead material was comprised of senescent plant material from both the current season and from previous seasons that was attached to crowns. Non-standing litter was not collected. Biomass was oven-dried for 24 hours at 40^{o}C, and then weighed. Aboveground net primary production (ANPP) was estimated from the peak live biomass clipped during the growing season (Biondini and Manske 1996). Multivariate analysis

of variance (MANOVA) was used to determine if burning, mowing, and the burning X mowing interaction affected live and dead aboveground biomass dynamics. To contrast any fire X mowing interaction with single factor results, MANOVAs were computed for burned vs. unburned plots in the absence of mowing, and mown vs. unmown plots in the absence of burning. Aboveground biomass data (live, dead) were log transformed prior to analysis to increase homogeneity of variances (Sokal and Rohlf 1995). To minimize spatial autocorrelation, the Greenhouse-Geisser adjustment was applied to "within-subjects" effects (Greenhouse and Geisser 1959, Littell et al. 1992). Analysis of variance (ANOVA) was used to determine in burning, mowing, and the burning X mowing interaction affected ANPP.

Community analyses

Bray-Curtis similarity coefficients (Bray and Curtis 1957) were calculated for the relative abundance of species (aboveground biomass) by plot and month, and square root transformed to balance the influence of dominant and rare species (Clarke and Warwick 2001). Analysis of similarity (ANOSIM) was then used to test for changes in the relative abundances of herbaceous species in response to burning, mowing, month, year, and their interactions. ANOSIM is a non-parametric permutation procedure based on ranking coefficients derived from similarity or dissimilarity matrices. ANOSIM calculates a test statistic (R) ranging from 0 to 1, where R=0 when there is an equivalent degree of similarity between and within groups, and where R=1 when all replicates within groups are more similar than any replicates from different groups (Clarke and

Warwick 2001). The statistic was then recomputed 5000 times/test using a Monte Carlo permutation (Clarke and Warwick 2001). Relatively few assumptions are made about the data, yielding a simple yet powerful analysis tool (Clarke and Warwick 2001). The particular species responsible for differences in overall community composition were determined using SIMPER. See Clarke and Warwick (2001) for a detailed discussion of ANOSIM and SIMPER, and criteria for selecting appropriate coefficients and transformations. PRIMER v5.2 (Plymouth Marine Laboratory, Plymouth, UK PL6 7DX) software was used for all community analyses.

The complex factorial design used in this experiment necessitated that ANOSIM be used in a sequential fashion, as there is no ANOSIM analog for repeated measures designs (Clarke and Warwick 2001). Separate ANOSIM procedures applied individually to each treatment combination failed to detect differences in relative abundance between the 1998 and 1999 growing seasons ($P > 0.05$); therefore, data from both years were pooled for subsequent analyses. To ascertain seasonal patterns of relative abundance on untreated plots, ANOSIM was applied to all unburned x unmown plots with "month" as the factor tested. Where differences between months were detected, SIMPER was used to determine which species contributing to the observed dissimilarities. All treatments were tested in a similar manner by month.

To test for interactions between burning (B) and mowing (M), a proxy variable "BxM" was created to identify each unique combination of B and M treatments. Similar to the approach used with factorial ANOVA designs, this interaction variable was tested prior to main effects during the months following initiation of combined treatments

(May-August). If BxM was significant ($P < 0.05$), tests of main effects for that month were disregarded (Sokal and Rohlf 1995).

Root and soil $\delta^{13}C$

$\delta^{13}C$ of plant roots obtained from ingrowth cores (see Chapter IV) were determined in order to establish the relative contributions of C_3 vs. C_4 plants to belowground biomass (Svejcar and Boutton 1985). $\delta^{13}C$ of soil organic carbon was quantified to assess the longer-term inputs of C_3 vs. C_4 plants to the soil carbon pool (see Chapter IV; Boutton 1996). As plots were sorted by species whose photosynthetic pathways were known, $\delta^{13}C$ was not determined on aboveground biomass. Roots (Chapter IV) and soils (Chapter V) were processed for $\delta^{13}C$ by combustion/gas chromatography using a Carlo-Erba EA-1108 elemental analyzer (CE Elantech, Lakewood, NJ) interfaced with a Delta Plus (Finnegan, Bremen, Germany) isotope ratio mass spectrometer as described by Nieuwenhuize et al. (1994). Dried roots were ground to a flour-like consistency in a Wig-L-Bug mill (Crescent Dental Manufacturing Co., Lyons, IL, USA) prior to nutrient analysis (Svejcar and Boutton 1985). Soils (0-10 cm and 10-20 cm depths) were collected from the center of a randomly selected subplot of each plot (Figure 4) at the end of each growing season (=August), sieved through a 2-mm screen to remove roots, dried at 60^{o}C, and finely ground through a centrifugal mill prior to analyses.

Results

Fire characteristics

Climate, fire temperatures and fuel loads were comparable during all prescribed fires, regardless of season or treatment year (Table 1).

Aboveground biomass

Regardless of treatment or year, species most commonly encountered across all treatments throughout the study were the annual *Bromus japonicus,* perennials *Nasella leucotricha, Bouteloua curtipendula*, *Buchloë dactyloides*, and *Bothrichloa laguroides* ssp. *torreyana* and forbs *Solanum elaeagnifolium*, and *Ambrosia psilostachya*. *Hilaria berlangeri, Sporobolus cryptandrus, Echinochloa crus-pavonis, Leptoloma cognatum, Aristida purpurea* var. *longiseta*, *Poa arachnifera*, and occasional *Prosopis glandulosa* seedlings were also recorded, although in negligible quantities.

Detailed MANOVA summaries of aboveground live biomass response are given in Appendix I, Tables A1-A12. There was a two-way interaction between cool-season burning and mowing (Table A1) such that aboveground biomass on burned x ungrazed plots was nearly twice that of any other treatment combination in both years (Figure 5a). Treatment year had independent and significant "between subjects" effects on aboveground live biomass (Table A1), with 1999 (=near normal precipitation) yielding 1.5X more biomass than 1998 (=drought year) throughout the entire growing season (Figure 5b, 6a-b).

Table 1. Fire and climate characteristics for cool season (March 1998, February 1999) and warm season (October 1998) prescribed fires. Fire temperatures were collected at 0, 10, 30, and 100 cm above the plots. For March 1998 only, soil temperatures 1 cm below the surface were measured in each plot.

	----------Cool Season Fire----------		**Warm Season Fire**
Characteristic:	**March '98**	**February '99**	**October '98**
Air Temp. (^{o}C)	29	19	29
RH (%)	33	33	28
Mean Wind Speed (mph)	6.5	5.5	8.8
Peak Fire Temps. (^{o}C)			
100 cm	367	222	201
30 cm	608	528	595
10 cm	609	639	656
0 cm	421	777	626
-1 cm	22	n/a	n/a
Avg. Fire Temps. (^{o}C)			
100 cm	49	29	49
30 cm	80	55	70
10 cm	106	82	125
0 cm	90	103	128
-1 cm	17	n/a	n/a
Avg. Fuel Load (g/m^{2})	295	273	254
Live Biomass (g/m^{2})	43	18	25

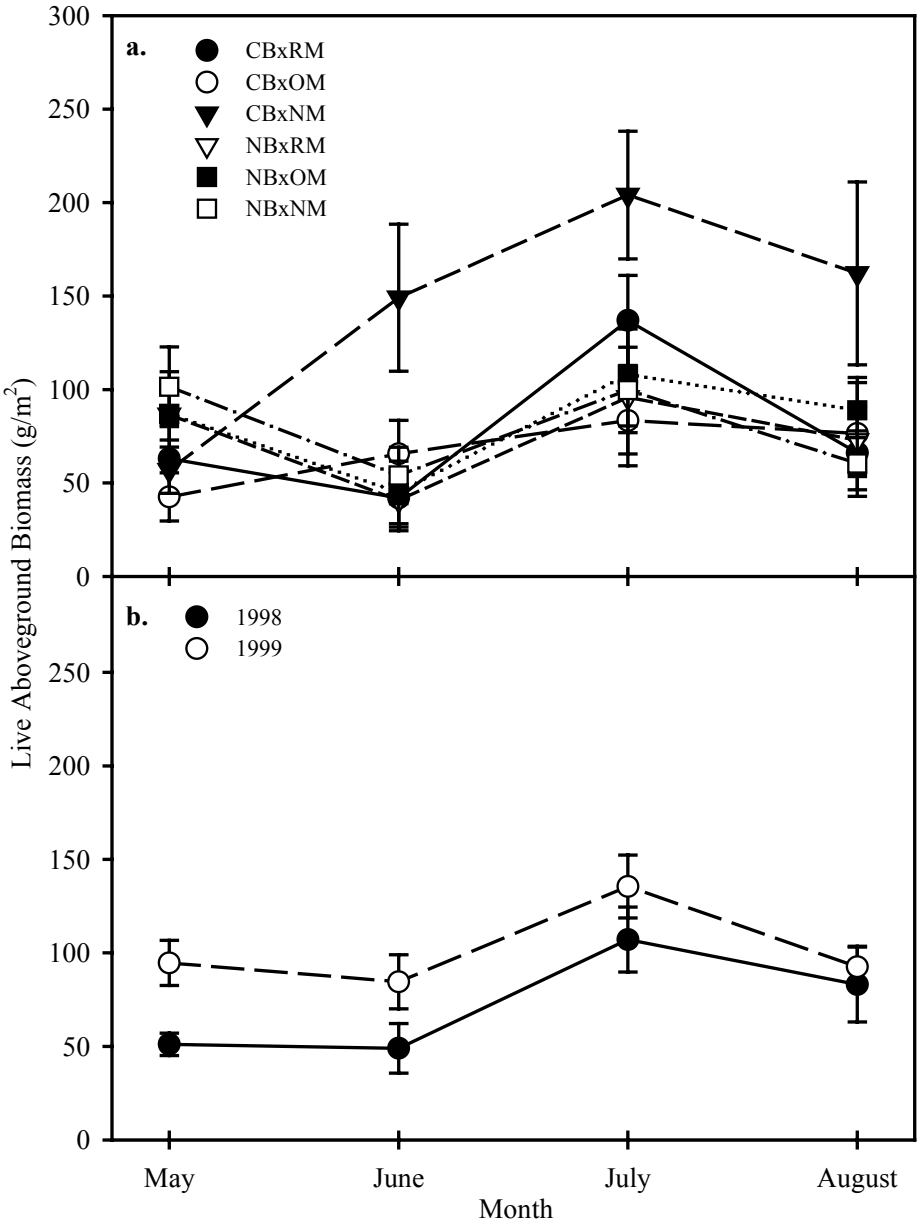

FIG. 5. Aboveground live biomass (all species combined) responses to (a) interactive effects of prescribed spring fire and mowing averaged over two years (1998-1999) and (b) climate. CB = cool season burn, NB = non-burned controls, RM = repeatedly mown, OM = once mown, NM = non-mown controls. Detailed statistical results are provided in Appendix I, Table A1.

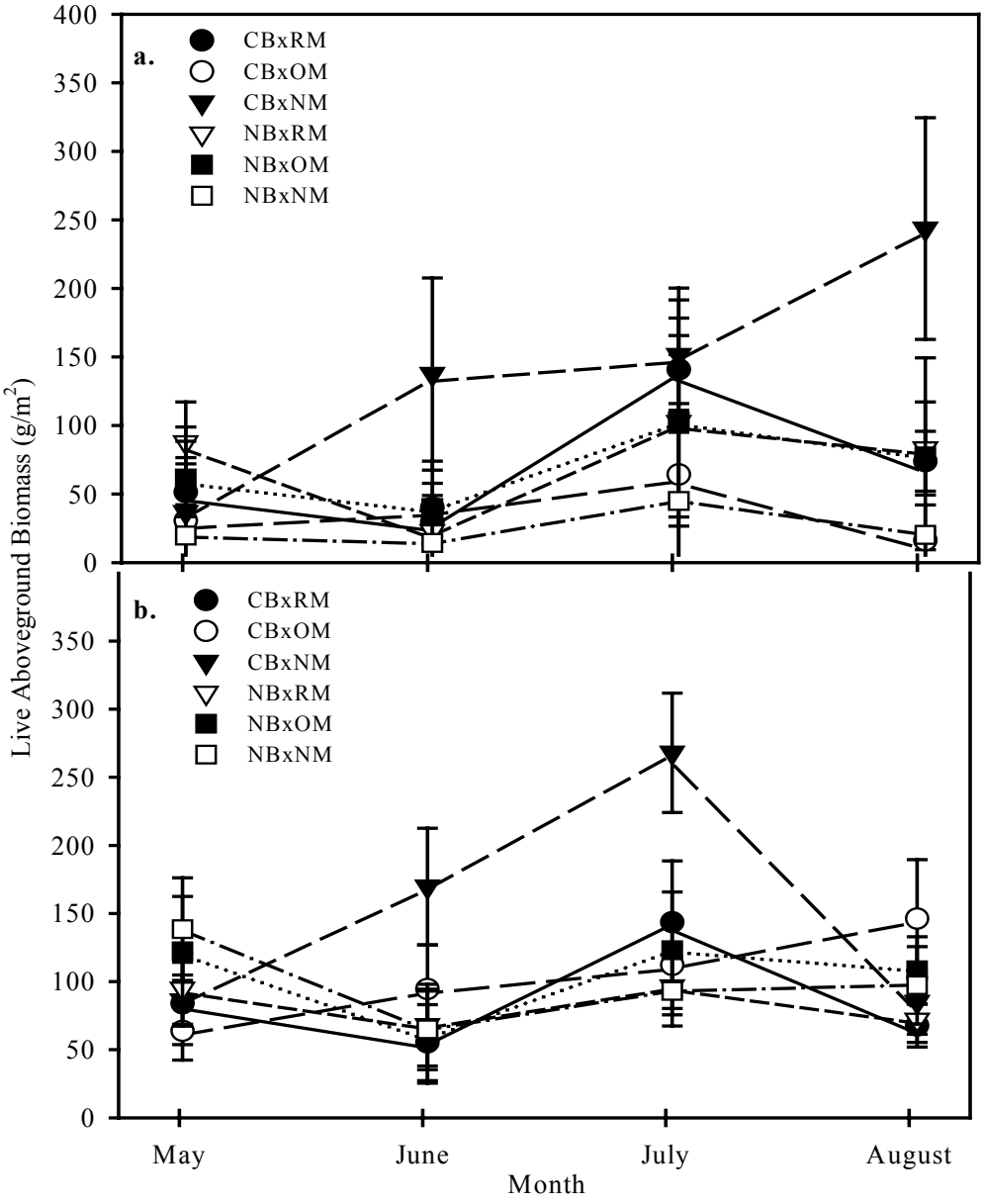

FIG 6. Interactive effects of fire and mowing on aboveground live biomass during (a) a drought year (1998) and (b) a year with near normal precipitation (1999). The effects of climate were independent ($P > 0.05$) of fire and mowing treatments (Appendix I, Table A1). CB = cool season burn, NB = non-burned controls, RM = repeatedly mown, OM = once mown, NM = non-mown controls. Detailed statistical results are provided in Appendix I, Table A1.

The main effect of mowing had significant "between subjects" effects such that standing dead biomass on unmown plots was three times greater than on once mown or repeatedly mown plots, which did not differ (Figure 7a, Table A2). Similarly, cool season burning had significant and independent "between subjects" reductions in standing dead biomass (Figure 7b, Table A2). There were no other main effects of interactions affecting standing dead biomass (Table A2).

To examine the potential effects of burning season, aboveground biomass on plots burned in October of 1998 (= warm season fire) was contrasted with that on plots burned in March of 1999 (= cool season fire) and on unburned, unmown control plots in 1999. Burning in either season had similar within season effects on aboveground live biomass for all species combined (Table A3) though warm season burning advanced the mid-summer spike one month earlier than cool-season burning (Figure 8a). Both fall and spring burning reduced standing dead biomass relative to unburned control plots (Table A4, Figure 8b).

There was a two-way interaction between cool season prescribed fire and mowing (Table A5) for ANPP (estimated from peak live standing crop) such that burned and unmown plots produced more than 1.5X the ANPP of all other treatments (Figure 9), which did not differ (Table A5). ANPP was not statistically different ($P > 0.05$) between treatment years ($ANPP_{1998}$ = 1550 ± 212 kg/ha, $ANPP_{1999}$ = 1844 ± 138 kg/ha; Table A5). ANPP in 1999 on plots burned in October of 1998 (3080 ± 505 kg/ha) was similar to that on plots burned in February of 1999 (2844 ± 399 kg/ha), and exceeded ANPP on non-burned controls (1768 ± 152 kg/ha; Table A6).

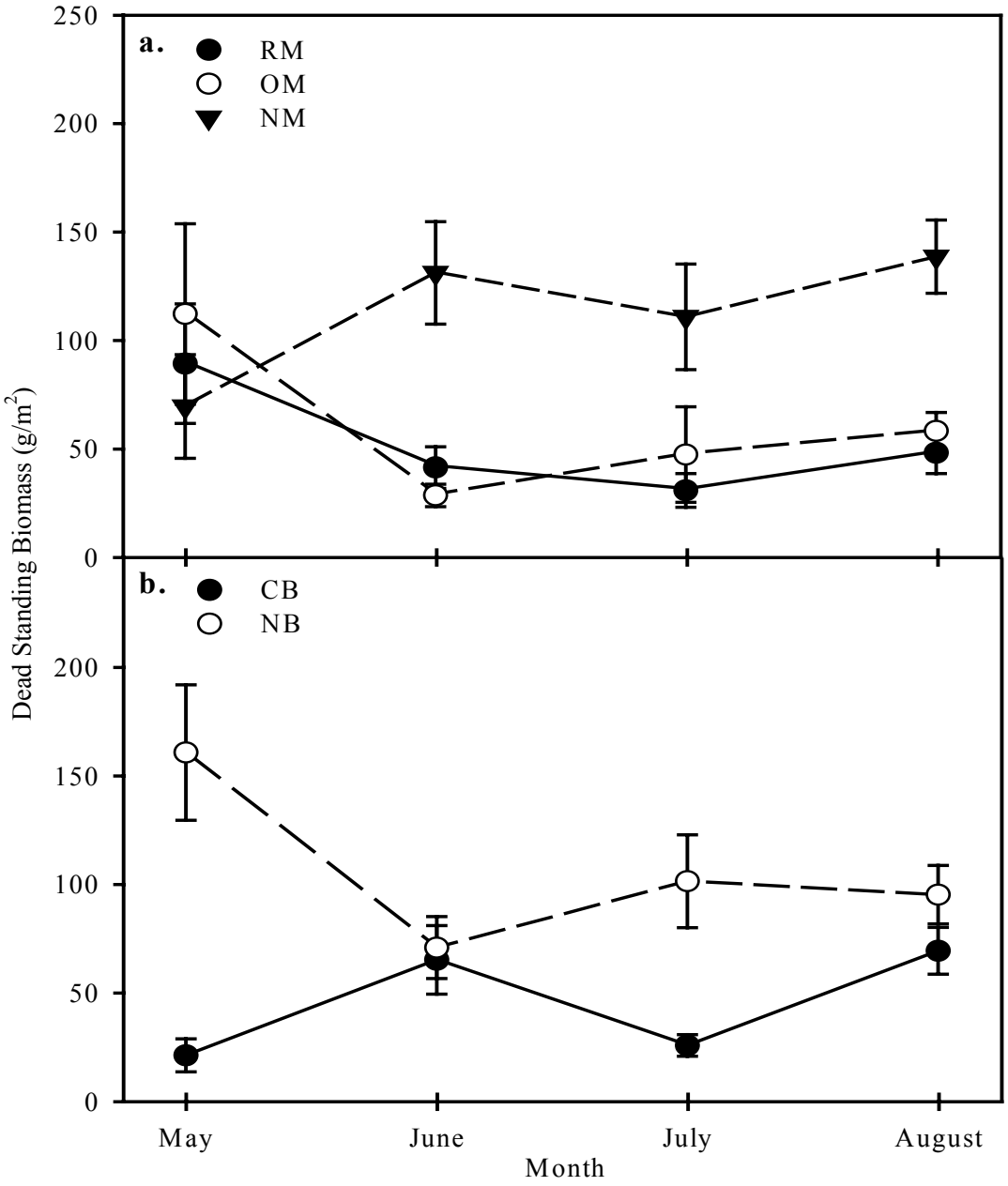

FIG. 7. Effects of (a) mowing and (b) cool season fire on standing dead biomass ("between subjects"). CB = cool season burn, NB = non-burned controls, RM = repeatedly mown, OM = once mown, NM = non-mown controls. Detailed statistical results are provided in Appendix I, Table A2).

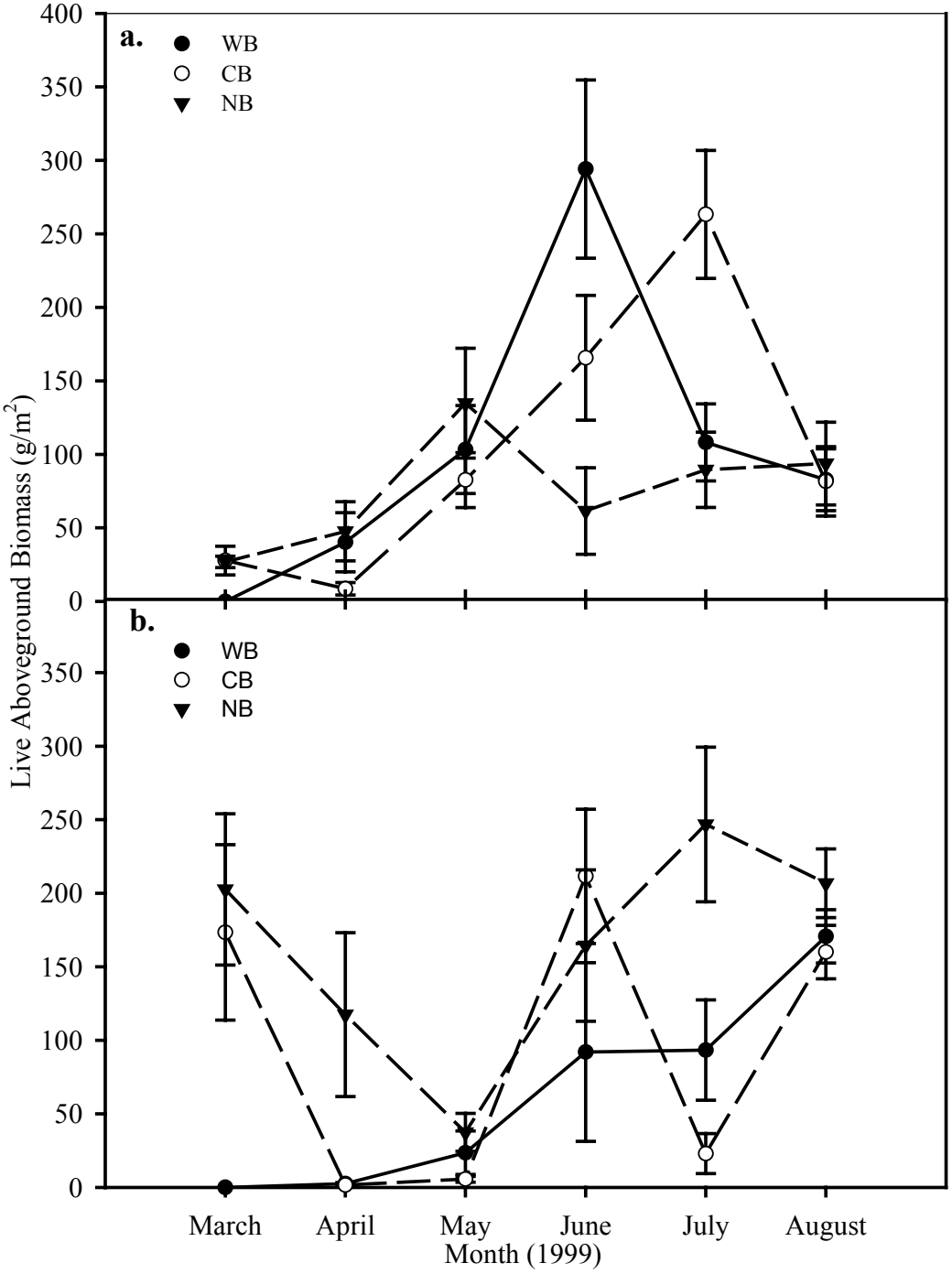

FIG. 8. Effects ("between subjects") of fall (October 1998) and spring (February 1999) prescribed fire on aboveground (a) live and (b) standing dead biomass during 1999. Detailed statistical results are presented in Appendix I, Tables A3-A4). WB = warm season burn, CB = cool season burn, NB = non-burned controls.

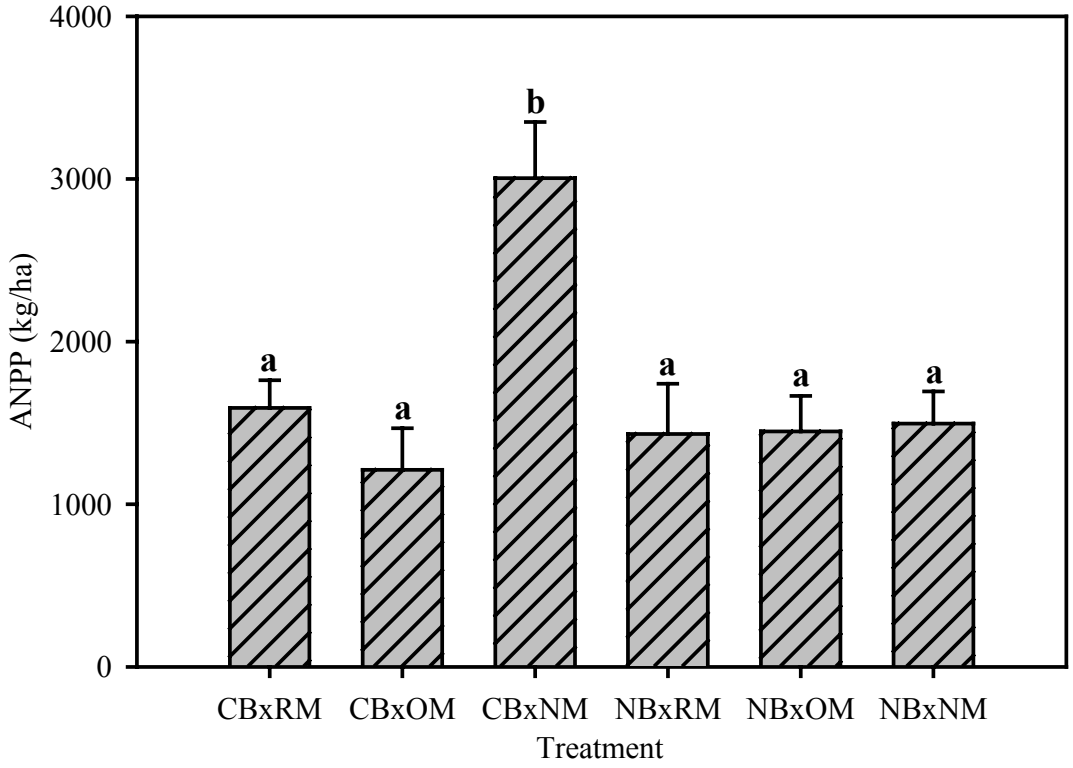

FIG. 9. Interactive effects of cool season prescribed fire and mowing on aboveground net primary productivity (ANPP). ANPP is estimated from peak live standing crop of all herbaceous species combined. Data (mean ± S.E.) are pooled over two years (1998-1999), as there were no significant differences ($P > 0.05$) between years. Different letters above bars denote significant differences ($P < 0.05$) between treatment combinations. CB = cool season burn, NB = non-burned controls, RM = repeatedly mown, OM = once mown, NM = non-mown controls. Detailed statistical results are presented in Appendix I, Table A5).

Forbs (primarily *Solanum elaeagnifolium* and *Ambrosia psilostachya*) comprised 25% to 83% of aboveground live biomass in burned x unmown plots, 11% to 39% in all other treatments, and exhibited the same two-way interactions observed for all species combined (Table A7, Figure 10). The "within-subjects" analyses for all species and forb aboveground live biomass (Tables A1, A7) revealed a three-way interaction between cool-season burning, mowing, and treatment year such that the increases on burned x unmown plots began in June rather than May for 1998, though the overall shape and magnitude of the response was comparable. Warm season burning (October 1998) had significant "within season" effects (Table A12) on forb aboveground biomass (Figure 11) that tracked the response of all species combined (Figure 8a). Warm season burning had no significant "between subjects" effects on forb aboveground biomass (Table A12).

Bromus japonicus exhibited the same response to climate as all species combined, with nearly twice the aboveground live biomass in 1999 than in 1998 (Table A8, Figure 12a, c). Cool season burning adversely affected annual *Bromus japonicus*, reducing its peak biomass and seasonal production by 70% and 60%, respectively (Table A8, Figure 12b, c). Cool season burning shifted the peak aboveground biomass of the C_4 grass *Bouteloua curtipendula* from August to July for both years (Figure 13), but did not significantly modify overall seasonal totals (Table A10). Other than those described above, there were no significant ($p < 0.05$) main effects or interactions affecting aboveground live biomass of individual species (Tables A7-A16).

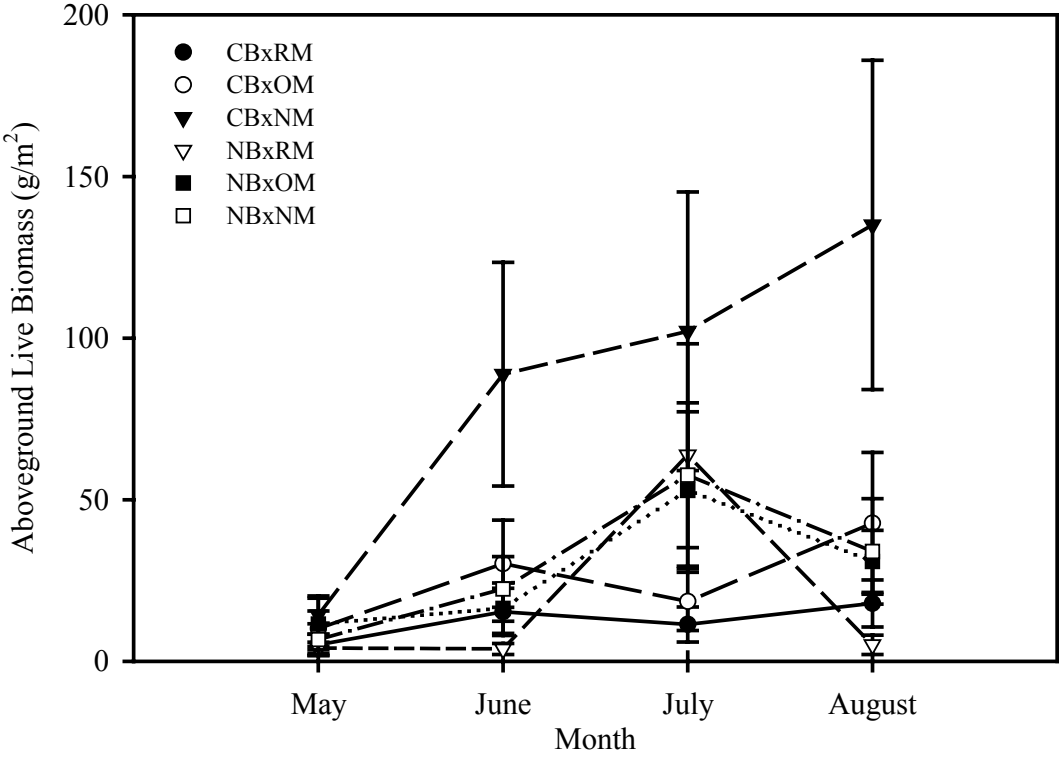

FIG. 10. Interactive effects ("between subjects") of cool season prescribed fire and mowing on aboveground live biomass of forb species (primarily *Solanum elaeagnifolium* and *Ambrosia psilostachya*). CB = cool season burn, NB = non-burned controls, RM = repeatedly mown, OM = once mown, NM = non-mowed controls. As treatment year was not statistically significant ($P > 0.05$), data are pooled over 1998 and 1999 growing seasons. Detailed statistical results are presented in Appendix I, Table A7.

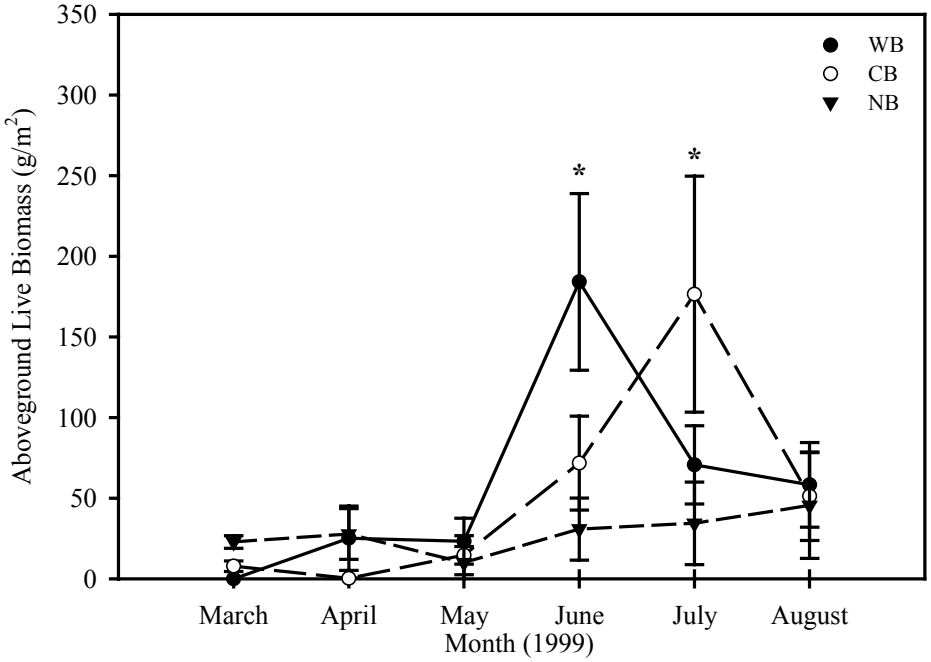

FIG. 11. Effects of warm season (October 1998) and cool season (February 1999) on aboveground live biomass of forb species (primarily *Solanum elaeagnifolium* and *Ambrosia psilostachya*) during the 1999 growing season. Forb biomass was significantly lower ($P < 0.05$) on non-burned control plots than on warm season or cool season burned plots ("between subjects"), which did not differ. WB = warm season burn, CB = cool season burn, NB = non-burned controls. Detailed statistical results are presented in Appendix I, Table A12).

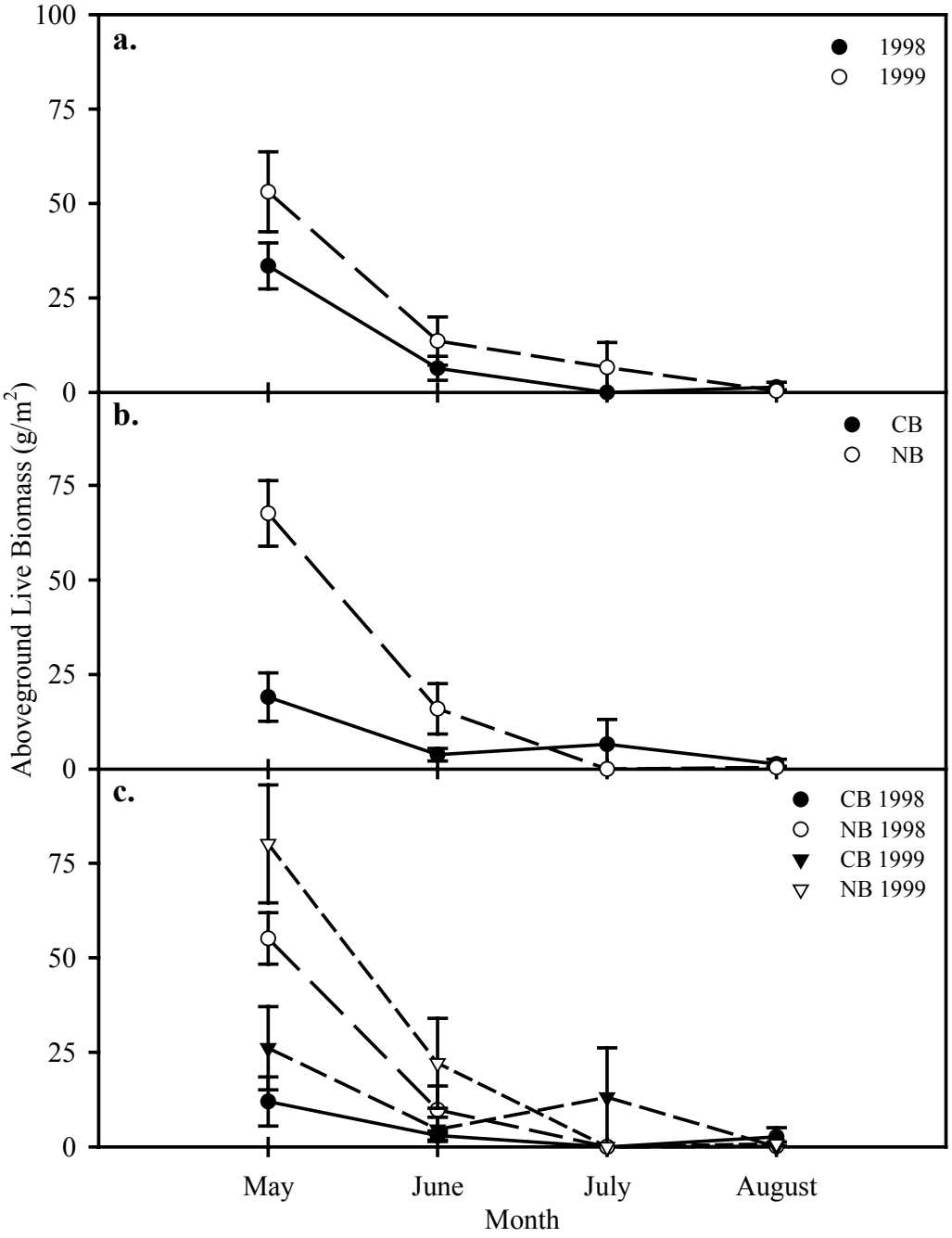

FIG. 12. *Bromus japonicus* aboveground live biomass response to (a) treatment year (1998, 1999), (b) cool season burning, and (c) burning effect expressed over treatment year effect. Treatment year and burning effects were independent. CB = cool season burn, NB = non-burned controls. Detailed statistical results are presented in Appendix I, Tables A8.

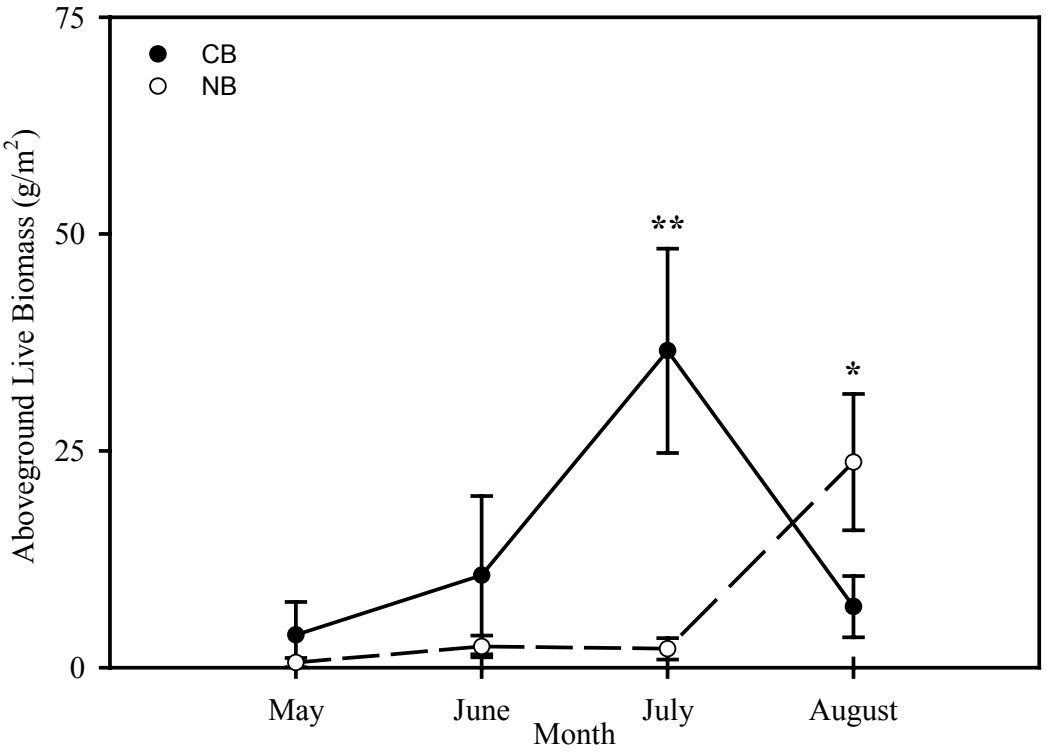

FIG. 13. Effects of cool season prescribed fire on aboveground live biomass of *Bouteloua curtipendula* in 1998 & 1999. CB = cool season burn, NB = non-burned controls. Burning had no effect on total growing season biomass ("between subjects"; $P < 0.05$). * and ** denote significant "within-season" effects ($P < 0.05$, $P < 0.01$, respectively). Detailed statistical results are presented in Appendix I, Table A10.

Single factor MANOVAs for cool season burning (unmown plots only) and mowing (unburned plots only) were contrasted with the full factorial fire X mowing (Tables A17-A18). The single factor MANOVA for burning revealed a significant "between subjects" effect of cool season fire such that ANPP for burned X unmown plots was 84% greater than unburned X unmown plots (Table A17). The single factor MANOVA for mowing did not detect any differences between mown X unburned and unmown X unburned plots (Table A18).

Community analyses

Four transient floristic assemblages (based on relative abundance of herbaceous species) were detected on control (non-mowed, non-burned) plots during both years: March, April, May/June, and July/August (Table 2). On treated plots, there was a burning x mowing interaction in May such that the composition of burned X unmown and burned X once-mown plots was significantly different from all unburned plots (Table 3). Burned X repeatedly mown (at that point in the season, twice-mown) plots did not differ from any treatment (Table 3). SIMPER analysis indicated a suppression of *Bromus japonicus* and stimulation of *Nasella leucotricha* and forb species on the burn X unmown and burn X once mown plots (Table 3). There were no burn X mown interactions for any other months (Table 3). Mowing had no detectable effect on the relative abundance of herbaceous species (Table 4). Burning in either season resulted in significant (though short-lived) changes to community composition (Tables 5-6). In the month following burning, the relative abundance of all species was reduced, particularly

Table 2. ANOSIM and SIMPER results discriminating within-season species assemblages on control (unburned, unmown) plots. "None" indicates no particular species was particularly associated with that treatment. Years (1998 & 1999) were pooled. Global = overall test of dissimilarity (analogous to ANOVA); paired tests follow (analogous to mean separation tests). R = test statistic indicating relative dissimilarity (0 to 1, with 1 = identical composition between groups). "*" denotes significant ($P < 0.05$) dissimilarity between groups. Percentages reflect proportion of dissimilarity attributable to each species.

Month:	**R**	*P*	Species Differentiation -SIMPER, (% of Dissimilarity)
Global	**0.246**	*<0.001* *	n/a
March vs. April	**0.428**	*0.024**	March – none April - Forb spp (47%), *Bromus japonicus* (27%), *Nasella leucotricha* (26%)
April vs. May	**0.480**	*0.002**	April – Forb spp (22%) May/June – *Bromus japonicus* (34%), *Nasella leucotricha* (26%)
May vs. June	**0.086**	*0.125*	n/a
June vs. July	**0.283**	*0.009**	May/June – *Bromus japonicus* (23%) July/August – *Nasella leucotricha* (25%), *Bouteloua curtipendula* (18%), Forb spp. (18%)
July vs. August	**-0.01**	*0.491*	n/a

Table 3. ANOSIM and SIMPER results discriminating within-season species assemblages for burning X mowing interactions. NB = unburned, CB = cool season burn, NM = unmown, OM = mown once, RM = repeatedly mown. "None" indicates no particular species was associated with that treatment. March and April preceded the implementation of both treatments; thus they are not shown. Years (1998&1999) were pooled. Global = overall test of dissimilarity (analogous to ANOVA); paired tests follow (analogous to mean separation tests). R = test statistic indicating relative dissimilarity (0 to 1, with 1 = identical composition between groups). "*" denotes significant ($P < 0.05$) dissimilarity between groups. Percentages reflect degree of dissimilarity attributable to each species.

Month:	Global/ Pairwise Tests	**R**	*P*	Species Differentiation - SIMPER, (% of Dissimilarity)
May/June	**Global**	**0.052**	***0.004****	CBxNM/ CBxOM: Forb spp. (14%), *Nasella leucotricha* (24%)
	NBxRM v. NBxNM	**0.057**	*0.075*	
	NBxRM v. CBxRM	**0.037**	*0.129*	
	NBxRM v. NBxOM	**-0.034**	***0.852***	
	NBxRM v. CBxNM	**0.083**	*0.017**	CBxRM: none – intermediate
	NBxRM v. CBxOM	**0.040**	*0.122*	
	NBxNM v. CBxRM	**0.119**	*0.015**	All other treatments: *Bromus japonicus* (47%)
	NBxNM v. NBxOM	**0.014**	*0.267*	
	NBxNM v. CBxNM	**0.143**	*0.009**	
	NBxNM v. CBxOM	**0.204**	*0.001**	
	CBxRM v. NBxOM	**0.041**	*0.126*	
	CBxRM v. CBxNM	**0.007**	*0.336*	
	CBxRM v. CBxOM	**-0.039**	*0.930*	
	NBxOM v. CBxNM	**0.07**	*0.048**	
	NBxRM v. CBxOM	**0.052**	*0.103*	
	CBxNM v. CBxOM	**-0.003**	*0.476*	
July/August	**Global**	**0.008**	***0.260***	n/a

Table 4. ANOSIM and SIMPER results discriminating within-season species assemblages for main effect of mowing. Years (1998 and 1999) were pooled. R = test statistic indicating relative dissimilarity (0 to 1, with 1 = identical composition between groups). "*" denotes significant ($P < 0.05$) dissimilarity between groups.

Month:	**R**	*P*	Species Differentiation -SIMPER, (% of Dissimilarity)
March	**-0.036**	***0.752***	n/a
April	**0.067**	***0.139***	n/a
May/June	**0.021**	***0.080***	n/a – burning x mowing interaction (Table 2)
July/August	**0.016**	***0.115***	n/a

Table 5. ANOSIM and SIMPER results discriminating within-season species assemblages for main effect of cool season burning. NOBN = unburned controls, CSBN = cool-season burning. "None" indicates no particular species was associated with that treatment. Years (1998 and 1999) were pooled. R = test statistic indicating relative dissimilarity (0 to 1, with 1 = identical composition between groups). "*" denotes significant ($P < 0.05$) dissimilarity between groups. Percentages reflect proportion of dissimilarity attributable to each species.

Month:	**R**	*P*	Species Differentiation -SIMPER, (% of Dissimilarity)
March	**-0.006**	***0.459***	n/a prior to application of prescribed burn
April	**0.364**	***0.001****	CSBN: none NOBN: *Bromus japonicus* (40%), Forb spp. (35%), *Nasella leucotricha* (21%)
May/June	**0.093**	***0.001****	CSBN: *Nasella leucotricha* (24%), Forb spp. (17%), *Digitaria californica* (11%), *Bouteloua curtipendula* (6%) NOBN: *Bromus japonicus* (35%)
July/August	**-0.001**	***0.457***	n/a

Table 6. ANOSIM and SIMPER results discriminating within-season species assemblages for warm season burning (1999 only). NOBN = unburned controls, WSBN = warm-season burning. Years (1998 and 1999) were pooled. R = test statistic indicating relative dissimilarity (0 to 1, with 1 = identical composition between groups). "*" denotes significant ($P < 0.05$) dissimilarity between groups. Percentages reflect proportion of dissimilarity attributable to each species.

Month:	**R**	*P*	Species Differentiation -SIMPER, (% of Dissimilarity)
March	**0.768**	***0.001****	WSBN: *Nasella leucotricha* (20%) NOBN: *Bromus japonicus* (80%)
April	**-0.156**	***0.897***	n/a
May/June	**0.167**	***0.035****	WSBN: *Nasella leucotricha*(35%), Forb spp. (14%), *Bouteloua curtipendula* (5%) NOBN: *Bromus japonicus* (39%)
July/August	**-0.032**	***0.591***	n/a

Bromus japonicus. However, burned plots quickly recovered and thereafter followed the trends of unburned plots. Significant burn effects in May were not considered, as there was a significant burn X mowing interaction for that month (Table 3).

C_3:C_4 aboveground biomass and root/soil $\delta^{13}C$

Mowing had significant "between subjects" effects on the ratio of C_3 to total (C_3 + C_4 plants) aboveground biomass throughout the growing season of each year (Table A19, Appendix I), such that 90% of the biomass on unmown plots was from C_3 plants, compared to 69% and 73% on repeatedly-mown and once-mown plots, respectively. Regardless of treatment, the contribution of C_3 plants to C_4 aboveground biomass declined from 92% to 67% as the growing season progressed (Figure 14, Table A19). The ratio of C_3 grass to total (C_3 + C_4) grass biomass mirrored this decline, dropping from 91% to 55% as the season progressed (Figure 14, Table A20) largely due to declines in *Bromus japonicus* biomass (Figure 12b). There were no other significant interactions or main effects for C_3 plants relative to all plants (Table A19-A20). Growing season root $\delta^{13}C$ tracked trends in aboveground biomass (Figure 14, Table A21, Appendix I), with root biomass becoming significantly more C_4-like (less negative values) as the growing season progressed. There were no other significant interactions or main effects for root $\delta^{13}C$ (Table A21).

Warm season burning in October of 1998 had significant "between subjects" effects (Table A22) on C_3 to total (C_3 + C_4 plants) aboveground biomass. Plots burned in October of 1998 had consistently greater C_3 to total (C_3 + C_4 plants) aboveground

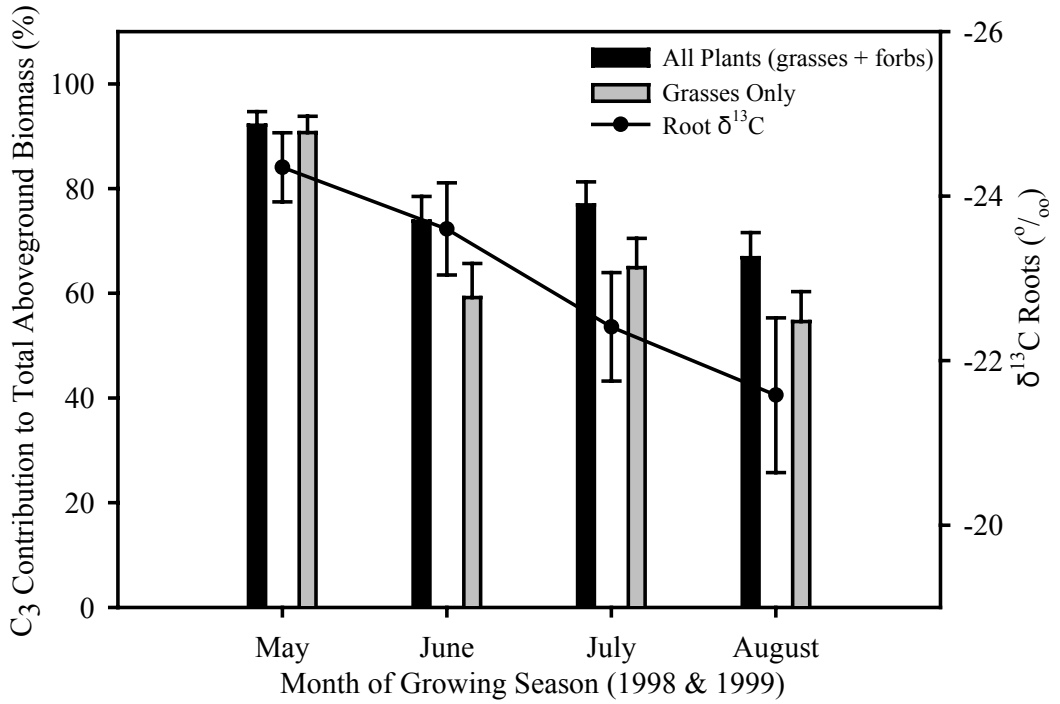

FIG. 14. Proportion (mean ± standard error) of C_3 to C_4 aboveground biomass (bars) and root $\delta^{13}C$ ($^{o}/_{oo}$) pooled over the 1998 and 1999 growing seasons. Roots were recovered from ingrowth cores (Chapter V). Above- and belowground data illustrate the increasing relative abundance of C_4 grasses in southern mixed grass prairie as the growing season progressed.

biomass ratios than plots burned in February of 1999 (Figure 9, Table A22), but no significant differences were detected between C_3 grass to total ($C_3 + C_4$) grass biomass (Table A23). Season of burning had no effect on root $\delta^{13}C$ (Table A24).

Soil $\delta^{13}C$ changed significantly with depth (Table A25), with 0-10 cm soils averaging –19.0±0.2 $^{o}/_{oo}$ versus –15.6±0.2 $^{o}/_{oo}$ for 10-20 cm soils (Table 7). No other interactions or main effects for $\delta^{13}C$ of soil organic carbon were significant (Tables A25-A26).

Discussion

Aboveground live biomass

These results indicate that fire X mowing interactions substantially influence aboveground live biomass dynamics of mixed grass prairie. Cool season burning in the absence of subsequent mowing greatly enhanced aboveground live biomass, a response consistent with many other single factor burning studies (Towne and Owensby 1984, Abrams et al. 1986, Briggs and Knapp 1995, Blair 1997). Mowing in the absence of fire had no effect on aboveground live biomass, also consistent with many grazing studies for northern mixed grass prairie (Lauenroth and Whitman 1977, Biondini and Mankse 1996, Biondini et al. 1998). However, mowing once or repeatedly following cool season burning reduced fire-induced aboveground live biomass gains to unburned levels. Assuming mowing reasonably mimics grazing, this interaction has important implications for mixed grass prairie ecology.

Table 7. $\delta^{13}C$ ($^{o}/_{oo}$) of soil organic carbon from cores collected in August 1998 and 1999. Values are means ± standard errors. No treatment interactions or main effects were significant ($P < 0.05$; Tables A19-A20, Appendix I). Depths were significantly different ($P < 0.0001$; Tables A19-A20). CB = cool season burn, WB = warm season burn, NB = unburned, NM = unmown, RM = repeatedly mown, OM = mown once.

	1998		1999	
Treatment:	$\delta^{13}C$ SOC (0-10cm)	$\delta^{13}C$ SOC (10-20cm)	$\delta^{13}C$ SOC (0-10cm)	$\delta^{13}C$ SOC (10-20cm)
All	-18.6±0.3	-15.9±0.3	-19.3±0.4	-15.3±0.3
CBxRM	-18.4±0.2	-15.5±0.2	-18.6±0.9	-13.7±1.2
CBxOM	-17.4±1.1	-14.3±0.2	-20.2±0.9	-16.0±0.4
CBxNM	-18.4±0.8	-15.8±0.1	-19.6±0.9	-15.7±0.5
WBxNM	n/a	n/a	-20.1±1.2	-16.0±0.6
NBxRM	-18.7±0.6	-16.5±0.8	-18.8±1.0	-15.6±0.4
NBxOM	-19.2±1.1	-16.2±0.8	-19.6±1.0	-15.4±0.3
NBxNM	-19.8±0.3	-16.6±0.8	-19.0±0.7	-15.9±0.8

Defoliation, whether by fire, grazing, or mowing, can stimulate compensatory growth by a variety of mechanisms (McNaughton 1983, Hulbert 1988), including increased incident radiation, and accelerated nutrient cycling (See Briske and Richards 1995 for a review). The occurrence and magnitude of compensatory growth is typically greater on sites that are infrequently defoliated (Oesterheld and McNaughton 1991, Seastedt et al. 1991, Milchunas and Lauenroth 1993, Briggs et al. 1994). The study site for this experiment had not been burned or grazed in more than 10 years, and had dense litter and senescent foliage accumulations at the onset of the study (Table 1). Mowing in the absence of burning would have removed both actively growing foliage and much of the detritus. Reductions in ANPP by consuming the former were evidently offset by the beneficial aspects of removing the latter (e.g., improved light conditions), resulting in an overall neutral response of ANPP to mowing in the absence of burning. Burning in spring and autumn when plants were quiescent, so relatively little live foliage would have been consumed. Burning appeared to consume surface litter and senescent foliage more intensively and extensively than did mowing, particularly the former, likely enhancing incident radiation and increasing surface soil temperatures early in the growing season. Thus, the net effect of burning on ANPP under these conditions was positive, and resulted in plots with relatively little detritus and large amounts of fresh foliage by late spring. As a result, subsequent mowing consumed primarily young, and therefore relatively efficient (Briske and Richards 1995), live foliage just prior to peak biomass production in early summer. Consequently, mowing eliminated the fire – induced ANPP pulse.

Hobbs et al. (1991) also demonstrated a fire X mowing interaction in tallgrass prairie, although their study examined aboveground biomass on grazed sites only. Prior to spring burning, Hobbs et al. (1991) mowed 2 x 2 m subplots to simulate "grazing patches", previously defoliated patches that grazing animals revisit and repeatedly defoliate (McNaughton 1984, Knapp et al. 1999). Ensuing fire behavior and spatial extent on these patches was reduced relative to other treatments, but the mosaic of mown patches was not apparent following the burn (Hobbs et al. 1991). The resulting uniform post-fire grazing on burned plots produced more aboveground biomass than the asymmetrical grazing of existing mown patches on unburned sites (Hobbs et al. 1991). In effect, prior defoliation by burning reduced the intensity of subsequent defoliation by grazing at the patch level. As the aboveground biomass portion of the Hobbs et al. (1991) study was conducted entirely on grazed plots, it is difficult to directly contrast their results with this study. However, the results of both studies suggest that fire and grazing interact to moderate extremes in ANPP.

The impact of mowing without burning on ANPP was neutral, consistent with the results of Lauenroth and Whitman (1977), Biondini and Manske (1996), and Biondini et al. (1998) for moderate livestock grazing in northern mixed grass prairie. Schuman et al. (1999) reported similar results for continuous light grazing of northern mixed grass prairie, but heavy continuous grazing reduced aboveground live biomass by 39%. Their results for heavy continuous cattle grazing suggest that the intensity and duration of the repeatedly mown treatments in this southern mixed grass prairie study likely mimicked moderate rather than heavy grazing.

Biondini and Manske (1996) reported an interaction between grazing and drought such that late summer ANPP was reduced on grazed mixed grass prairie during a drought year, though it was not sufficiently different to affect annual ANPP. No such interaction was detected in this study, despite 1998 being one of the driest summers on record for Texas. ANPP responded independently to the drought with a 30% decrease relative to the wetter (though still below average) 1999-growing season.

Seasonal community dynamics

Increasing evidence indicates that fire and grazing have dramatic short-term and long-term effects on community structure and seasonal dynamics (Abrams and Hulbert 1987, Collins 1987, Gibson and Hulbert 1987, Hulbert 1988, Gibson 1988, Collins and Glenn 1990, Heitschmidt 1989, Collins 1992, Noy-Meir 1995, Knapp et al. 1999). Wedin and Tilman (1993) and Wedin (1995, 1996) described the functional significance of community structure in grasslands, whereas Collins and Gibson (1990) suggested that patch level "micro-succession" and structural dynamics following disturbance have ecological consequences over broader scales.

This study illustrates a dynamic system in which the relative abundance of species changes dramatically and rapidly as the growing season progresses, with fire X mowing interactions having sizeable but transitory effects, whereas the extreme climatic variability observed during the study had no apparent impact. In the absence of burning or grazing, both 1998 and 1999 growing seasons began with a sparse *Bromus japonicus* monoculture in March, followed by a relatively dense growth of *Bromus*

japonicus/Nasella leucotricha with occasional forbs during April. During May and June, biomass of C_3 grasses peaked, and then began a steep decline. As xeric conditions developed in July and August, *Bromus japonicus* senesced, *Nasella leucotricha* slowly declined, and the C_4 perennial *Bouteloua curtipendula* and to a lesser extent *Buchloë dactyloides*, and *Bothrichloa laguroides* ssp. *torreyana* assumed dominance. Other warm-season grasses were evident during late summer, particularly *Digitaria californica, Sporobolus cryptandrus, Echinochloa crus-pavonis,* and *Leptoloma cognatum*, although in negligible quantities.

Both shoot and root production shifted from almost entirely C_3 grasses and forbs towards mixed C_3 /C_4 production by late summer, though C_3 plants were still more abundant at the end of the growing season. This C_3 dominance was confirmed by the near surface soil organic carbon (SOC) $\delta^{13}C$ values. However, $\delta^{13}C$ values for SOC 10-20 cm beneath the surface suggest past C_4 grass domination. This suggests that prior to fire and grazing exclusion, the site may have been dominated by the C_4 shortgrasses and midgrasses common on unprotected prairie sites in the region (Heitschmidt et al. 1985, Heitschmidt et al. 1987, Ansley and Jacoby 1998), and may currently be out of equilibrium with long-term vegetation patterns. The lack of treatment effects on C_3 /C_4 composition suggests that more frequent and/or intense fire and grazing events would be required to shift the site towards C_4 prevalence.

The continued production of C_3 plants into late summer, despite the xeric conditions that tend to favor C_4 grasses (Larcher 1995), was due to *Nasella leucotricha*. This perennial C_3 bunchgrass is very "C_4 -like" in its tolerance of hot and dry conditions

(Gould 1975, Whisenant 1984, Hicks et al. 1990). *Nasella leucotricha* was among the first species to begin growth in late winter, and the last to go dormant during the xeric conditions of late summer/early fall. Whisenant (1984) concluded that fall burns tend to favor *Nasella leucotricha* over warm season C_4 grasses, whereas spring fires benefit warm season perennials at the expense of *Nasella leucotricha*. Ansley et al. (1999) reported that repeated spring burning and clipping drastically reduced *Nasella leucotricha* in Low Rolling Plains mixed grass prairie, while fall burning had little effect. In contrast to the results of Whisenant (1984) and Ansley et al. (1999), fire and mowing had no significant effects on *Nasella leucotricha*, which was ubiquitous across treatments and months. This disparity may be a function of defoliation intensity, as Heitschmidt et al. (1989) reported decreased *Nasella leucotricha* under heavy continuous livestock grazing relative to moderate continuous grazing.

Both burning treatments had profound effects on the production and persistence of the perennial native forbs *Solanum elaeagnifoium* and *Ambrosia psilostachya* throughout the season. Likely through a combination of rhizome proliferation (Kingsbury 1964, Boyd and Murray 1982a,), and release from shading (Boyd and Murray 1982b, Vermeire and Gillen 2000), burning quadrupled forb biomass in early-summer, resulting in nearly double the total ANPP on burned X unmown plots relative to all other treatments. On burned plots that were subsequently mown, this pulse of forb aboveground biomass was reduced to unburned levels by late mid-summer. As warm season burned X unmown plots exhibited a similar profusion of aboveground forb biomass production, I can only speculate that a similar interaction following mowing

(drastic reduction) might occur, as this treatment combination was not applied. Stimulation of *Solanum elaeagnifoium* and *Ambrosia psilostachya* biomass production following fire is of concern for livestock producers, as the former is poisonous (Boyd et al. 1984) and the latter is seldom utilized (Vermeire and Gillen 2000). However, perennial grass production on burned and unburned plots was not affected by the production of these weedy species, a response that has been observed in other mixed grass prairie species (Vermeire and Gillen 2000). Furthermore, livestock tend to avoid both species if more palatable forage is available (Boyd et al. 1984, Vermieire and Gillen 2000). Except under extreme stocking rates, grazing animals are likely more selective than a lawn mower, so the extent to which grazers would reduce forb biomass as did mowing in the study, is debatable.

Both spring and autumn burning caused the near eradication of *Bromus japonicus*, an invasive exotic grass of relatively low forage value (Whisenant 1989), though the suppression mechanism likely differed. Warm-season burning removed the dense litter accumulation that is critical for subsequent *Bromus japonicus* germination (Whisenant 1990), whereas cool season burning, occurring after the emergence of most *Bromus japonicus* seedlings, likely caused direct mortality to actively growing plants. The cumulative effects of burning on the *Bromus japonicus* seed bank may explain the lower abundance of this weedy annual on nearby sites that are burned regularly.

The first year of this study coincided with one of the most severe short-term droughts on record for northern Texas (Chapter III, Figures 1-2), and while overall seasonal biomass was diminished, no intra-seasonal shifts in community structure were

detected. Although fire and grazing were driving community dynamics during spring and early summer, the effects of these disturbances had disappeared by late summer, as all plots were composed of a similar mixture of C_4 grasses, *Nasella leucotricha*, and forbs, and were indistinguishable the year following treatment. The resiliency of mixed grass prairie patch structure to fire, grazing, and drought has been widely observed (Dix 1960, White and Currie 1983, Engle and Bultsma 1984, Biondini and Mankse 1996, Biondini et al 1998, Schuman et al. 1999), suggesting that intense and repeated defoliation is required for dramatic and enduring shifts in community structure. The short-term fire and grazing interaction responses observed in this study does nothing to change this view presented by the single-factor studies.

The contrast between the fully factorial design with two single-factor experiments (burned vs. unburned plots in the absence of mowing, and mown vs. unmown plots in the absence of burning) revealed a broad gap in the results and subsequent interpretations from these two approaches. From an analysis and design perspective, this was as if there were two separate experiments being conducted on adjacent plots with all other factors (climate, soils, sampling methods) being equivalent for both experiments. Using the single factor approach, cool season fire nearly doubled ANPP, whereas mowing had no effect on ANPP. If we were to assume independence of fire and grazing effects, then the combined outcome would indicate that the increased ANPP following burning was unaffected by mowing. The dampening effect of mowing on fire-enhanced ANPP was revealed only by the factorial study. This study emphasizes

the importance of composite factors in regulating functional attributes of grasslands (McNaughton 1983), and the perils of single factor studies.

CHAPTER IV

EFFECTS OF FIRE AND GRAZING ON ROOT DYNAMICS

Introduction

Roots serve as the essential means by which plants acquire water and nutrients, store resources, and are physically anchored to a specific locale. At ecosystem scales, roots contribute a substantial proportion of the carbon being cycled annually (Vogt et al. 1996), as well as at least one third of global annual net primary productivity (Jackson et al. 1997). On global scales, fine root area exceeds leaf area by an order of magnitude in temperate grasslands, and fine root biomass and surface area are greater in grasslands than in any other biome (Jackson et al. 1997). The effects of disturbances such as grazing on grassland root systems have received considerable attention (e.g., Jameson 1963, Milchunas and Laurenroth 1993). Even so, there is little consensus on the effects of defoliation on root systems (Table 8). Milchunas and Laurenroth (1993) used multiple linear regression to analyze 276 published data sets to ascertain the relationship between grazing and root biomass. Contrary to expectations, there was neither a strong nor consistent relationship between grazing and root mass. Does this mean that roots are largely decoupled from the effects of disturbance (e.g., grazing), or that potential disturbance effects are masked by confounding variables such as topoedaphic variation, site history, and contrasting species-specific responses? Or, have differences in root

Table 8. Selected examples of the effects of fire and grazing on root production in grass dominated ecosystems. "Pot" = potted plant studies, **F** = fire, **G** = grazing, **C** = clipping, ↑ = treatment increased root parameter, ↓ = decreased root parameter, **NE** = no effect.

Author:	System:	Pot/Field:	Trt(s):	Parameter/Tech:	Units:	Root Production:
Benning and Seastadt 1997	Tallgrass prairie, USA	Field	**F + C**	Length/ Rhizotrons Biomass/ Cores and Monoliths	mm/mm^2 g/m^2	NE on root length; **C**, **F**, & **CxF** ⇑ total and dead biomass, NE on live roots
Geordiadis et al. 1989	East African savanna	Pot	**C**	Biomass/ Whole plant harvest	g/plant	⇓ biomass, NE on root:shoots ratio
Jameson 1963	Review of 25 studies from several systems	Pot	**C**	Biomass/ Whole plant harvest	g/plant	⇓ biomass
Kucera and Dalhman 1968	Tallgrass prairie, USA	Field	**F**	Biomass/ Cores	g/m^2	⇑ biomass on annually burned plots
McNaughton et al. 1998	Serengeti, Africa	Field	**G**	Biomass (live)/ Cores	g/m^2	NE on biomass
McNaughton and Chapin 1985	Serengeti, Africa	Pot	**C**	Biomass/ Whole plant harvest	g/plant	⇑ or NE depending on phosphate concentrations
Milchunas and Laurenroth 1989	Shortgrass steppe, USA	Field	**G**	Biomass/ Cores	g/m^2	⇓ biomass
Oesterheld and McNaughton 1991	Flooding pampa, Argentina	Pot	**C**	Biomass/ Whole plant harvest	g/plant	NE on biomass
Shackleton et al. 1988	Coastal grassland, southern Africa	Field	**F + G**	Biomass/Seq.Coring	g/m^2	**G**:⇓ biomass, **F**:NE biomass
Sims and Singh 1978*a, b*	10 central and western USA grasslands	Field	**G**	Biomass/ Cores	g/m^2	⇑ on cooler sites, NE on warmer sites
van der Maarel and Titlyanova 1989	Steppe, Russia & Sweden	Field	**C**	Biomass (live vs. dead)/ Monoliths	g/m^2	⇑ live roots under moderate **C,** ⇑ dead roots under moderate & high **C**

sampling methodologies confounded comparisons and prevented us from accurately measuring root response to disturbance? Furthermore, most studies have considered fire *or* grazing as a single independent disturbance factor. For grasslands, a more realistic approach would be to examine fire *and* grazing, and account for their interaction (Collins 1987, Collins and Gibson 1990, Hobbs et al. 1991, Noy-Meir 1995).

Whether a particular study found a "response" might, to some extent, be an artifact of the method used. Root system studies are notorious for their methodological limitations (Caldwell and Virginia 1989, Vogt and Persson 1990, Vogt et al. 1998, Smit et al. 2000, Box 2002). Böhm (1979) noted, "Root research under natural field conditions is a stepchild of science. The reason for this is primarily methodological. The known methods are tedious, time-consuming, and the accuracy of their results is often not very great." A variety of techniques are used to sample root systems, ranging from sophisticated imaging and tracer studies to core and monolith excavations (Bengough et al. 2000). These methods generally fall into two categories: *in situ* and destructive techniques (Böhm 1979), each with particular advantages and disadvantages (Bengough et al. 2000, Smit et al. 2000, Box 2002). An effective strategy for quantifying root system dynamics may be to use multiple techniques in concert. Caldwell and Virginia (1989) noted, "Bringing several approaches to bear on the same questions will allow strengths and weaknesses of different techniques to compensate one another." However, doubling the already daunting task of root sampling with a single technique is likely to dissuade most investigators, and this approach has rarely been adopted.

Models of root response to defoliation

Microcosm/ Individual Plant Model: Defoliation inhibits short-term root growth

In his review of 25 published studies of foliar clipping effects on individual grasses, Jameson (1963) provided compelling evidence that defoliation initially curtails root growth. This reduction in root growth observed in defoliated plants was attributed to preferential allocation of stored resources to leaves and restoring carbon gain capacity at the expense of root growth and maintenance. This view has persisted and has been echoed in more recent reviews (Briske and Richards 1995). However, most of the studies documenting decreases in root biomass with defoliation have been at the scale of individual potted plants.

Field/Ecosystem Model: Defoliation does not inhibit root growth

Citing more recent field and controlled environment studies which indicate that defoliation may have positive, negative, or neutral effects on root production (Table 7), McNaughton et al. (1998) argued that "if root growth is inhibited by defoliation, so also shoot growth will be inhibited" due to limitations on nutrient uptake. They contend that the variable responses of roots to defoliation invalidate the assumptions that form the basis for the traditional root response model. The meta-analysis of 276 grazing data sets by Milchunas and Laurenroth (1993) provides compelling support for the Field/Ecosystem model. Milchunas and Laurenroth (1993) failed to detect any single, generalized response of roots to grazing; positive, negative, and neutral (=no effect) effects were commonly observed. The lack of a generalized response may reflect

differences in scales of observation. In contrast to individual plant/pot studies, not all plants in an ecosystem study would be defoliated uniformly. Root biomass of the defoliated individuals may decrease in accordance with the individual plant model. However, undefoliated or less severely defoliated plants may respond by increasing their root biomass to take advantage of the resources made available by defoliation of other plants. Thus, the net result may be that moderate defoliation would have a neutral or positive effect on ecosystem root biomass. Even in cases of severe and extensive defoliation, the magnitude of decreases in root biomass predicted by the individual plant model may be dampened at the ecosystem level.

Experimental goals

As root growth and turnover play fundamental roles in ecosystem processes, and as there are opposing theoretical and empirical perspectives on the effect of fire and grazing on grassland root systems, a comprehensive investigation of root system response to fire, grazing and their interaction employing multiple root sampling techniques is needed. The goal of this study was to experimentally evaluate these competing models of root response using two methods for sampling roots: minirhizotrons and root ingrowth cores (Böhm 1979, Caldwell and Virginia 1989, Vogt et al. 1998), and contrast their results to determine if methodological bias may be contributing to the debate. Effects of fire, grazing, and their interaction on grassland root system dynamics were investigated using a factorial field experiment.

Methods

Chapter II provides a detailed description of the study site, experimental design and treatments.

Minirhizotron

Root length and turnover was measured monthly from March through August of 1997 and 1998 using minirhizotrons (Bland and Dugas 1988, Hendrick and Pregitzer 1996). In each plot, a minirhizotron (clear plastic tube 75 cm long x 5.08 cm inside diameter) was permanently inserted into the soil (45^{o} angle) to a vertical depth of 32 cm. The location of the minirhizotron within each plot was in the center of a randomly assigned block of four subplots (Figure 2) to minimize the influence that other sampling activities might have on root productivity. The aboveground portions of each minirhizotron were painted black, wrapped in insulated tape, and capped with a rubber stopper and aluminum can to prevent light and moisture from entering the tube. Minirhizotrons were installed in August of 1998 and allowed to equilibrate. Readings commenced in March 1998. Minirhizotron images were collected using a video camera system (Bartz BTC-2, Bartz Technology Company, Santa Barbara, CA). The Bartz system uses an indexing handle and reference images to locate specific depths, obviating the need for tube etchings. The camera was lowered to the maximum depth for each minirhizotron, and the position verified by comparison with a reference image. Images were collected sequentially on VHS videotape until the minimum depth was reached. Depths were recorded by reading the value off the index handle into a microphone

connected to the videocassette recorder. Individual roots observed in each 1.2-cm x 1.6-cm image were traced and classified as new (those not present the previous month), existing (root observed during prior sampling), or dead (roots observed in a previous month which are missing or have substantially darkened or exhibit other signs of decay), using RooTracker Version 1.1 (Duke University Phytotron, Durham, NC). This Macintosh-based software package allows individual roots to be followed over successive sampling dates, yielding root length and turnover by diameter class. Two additional categories were derived from these monthly measurements: root length recruitment (=new root length – dead root length), and live root length (existing root length + recruited root length).

Root ingrowth cores

Root biomass and length production were measured monthly from May through August using root ingrowth cores, a modified version of the ingrowth bag technique (Steen and Håkansson 1987, Steen 1988, Vogt et al. 1998). Ingrowth cores were permanently established within each plot in a randomly selected subplot. Each ingrowth core consisted of a soil column (35 cm deep x 8.9 cm diameter) filled with a root-free mixture of commercially available clay and sand soil (50:50 Hyponex Sandbox Sand + Hyponex Topsoil Mix). Each month, the center 5.08-cm (diameter) core of soil was collected with a hammer auger (AMS, Forestry Suppliers, Inc., Jackson, MS) in 0-15 cm and 15-30 cm depth increments. The remaining soil in the column was removed and discarded. The hole was then refilled with the root-free soil mixture and left until the

next sampling period. The collected soil samples were stored in a refrigerator (ca. 7^{o}C) to minimize post-collection decay and desiccation and prevent biomass loss associated with freezing (Price and Heitschmidt 1989). A hydropneumatic elutriation system (Gillison's Variety Fabrication, Inc., Benzonia, MI) was used to extract roots from ingrowth cores (Smucker et al. 1982). Primary and secondary sieve sizes were 760 μm and 410 μm, respectively. Hydropneumatic elutriation ("root washing") is an efficient method for extracting roots, and recovers roots at rates comparable with other more time-consuming and labor-intensive methods (Hubbard et al. *in prep*). Extracted roots were separated from organic debris and scanned at 400 dpi resolution (Hewlett Packard Scanjet 3) to determine root length by diameter class using image analysis software (WinRhizo Version 3.8 Régent Instruments, Inc, Montreal, Quebec, Canada). Following scanning, roots were oven dried at 60^{o}C for 48 hours and weighed to determine biomass. Because roots were utilized for isotopic and nutrient analyses (Chapters III and V), they were not ashed.

Statistical analyses/design

Multivariate analysis of variance (MANOVA) was used to analyze these data as a three-factor experiment (Fire x Graze x Treatment Year) with repeated measures (Sokal and Rohlf 1995). Because the monthly sampling variable is inherently ordinal (=ranked), orthogonal contrasts (Littell et al. 1992) were used to compare the overall trends of each treatment combination through the entire growing season. In this manner, treatment effects could be emphasized over differences merely due to seasonal changes

in climate. Chapter II provides a more detailed description of these analyses.

To contrast the production estimates obtained by each method, correlation coefficients were computed between "new" root length observed in minirhizotrons and biomass and root length density recovered from ingrowth cores. Some authors (Heerman and Juma 1993) have assumed a particular depth of field for minirhizotron images to permit calculations of root length density (cm per cm^{-3}). While assuming a particular depth of view allows direct comparisons between coring methods via hypothesis testing (e.g., ANOVA), the arbitrary nature of the volume estimates has been questioned (Smit et al. 2000). Consequently, I restricted my comparisons to correlations and qualitative evaluations. As the data did not meet the bivariate normal assumptions required for Pearson's product-moment correlations, the non-parametric equivalent was used. Therefore, potential correlations between new root area density (cm root length per cm^2 of visible minirhizotron tube) and root biomass production (grams per m^2 to 30 cm depth of ingrowth core) and root length density (cm root length per cm^3 of ingrowth core) were examined using Kendall's tau correlation coefficients (Sokal and Rohlf 1995).

Results

Minirhizotron

Detailed statistical results are presented in MANOVA tables A27-A36 in Appendix I. As treatment year had no effect on root parameters measured with minirhizotrons, data were pooled over both years (1998, 1999) of the study. The

main effect of spring burning had significant "within subjects" effects on root length production and mortality (Tables A27-A28), such that burning initially quadrupled production, then subsequently doubled mortality, relative to unburned plots (Figure 15). The main effect of mowing had a significant "within subjects" effect on root length mortality (Table A28) expressed as a 60% reduction on once-mown and repeatedly mown plots immediately following the initial treatment (Figure 15). There were no other significant interactions or main effects for root length production and mortality (Tables A27-A28).

There was a two-way interaction between spring burning and mowing driving root length recruitment (production-mortality), such that overall seasonal recruitment totals increased 2.25 – 3.5X on plots that were burned, mown, or both, relative to undefoliated controls ("between subjects"; Table A29, Figure 16). Root length recruitment on all burned plots and mown X unburned plots increased 3X and 5X, respectively, during the month following the initial defoliation (April and May, respectively), relative to other treatments, which were equivalent. The effects of burning and mowing on recruitment were not additive; burned plots that were subsequently mown did not exhibit a second pulse of recruitment following the mowing treatment, and repeatedly mown plots did not respond after the initial treatment (Table A29, Figure 16). Recruitment decreased across all treatments as the growing season progressed (Table A29).

To contrast the spring burning X grazing interaction with single factor perspective, MANOVAs were calculated independently for the main effects of burning

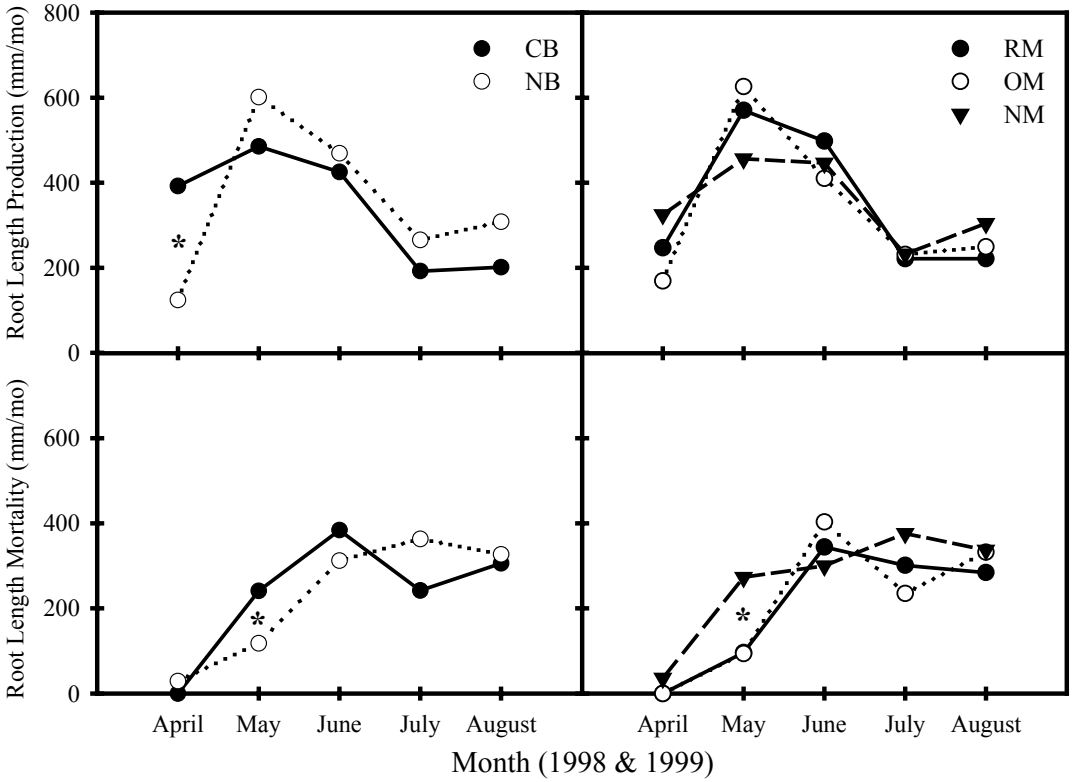

FIG. 15. Within-season ("within-subjects") effects of spring burning on root length production, and root length mortality during the 1998 and 1999 growing seasons. Overall seasonal rates ("between subjects") were not affected ($P > 0.05$). Root length (mm) is expressed over the viewable area of the 0-30cm depth of the minirhizotron (5189 mm^2). CB = cool season burn, NB = non-burned controls, RM = repeatedly mown, OM = once mown, NM = non-mown controls. * = $P < 0.05$ for "within subjects" effects. Detailed statistical results are presented in Appendix I, Tables A27-A28.

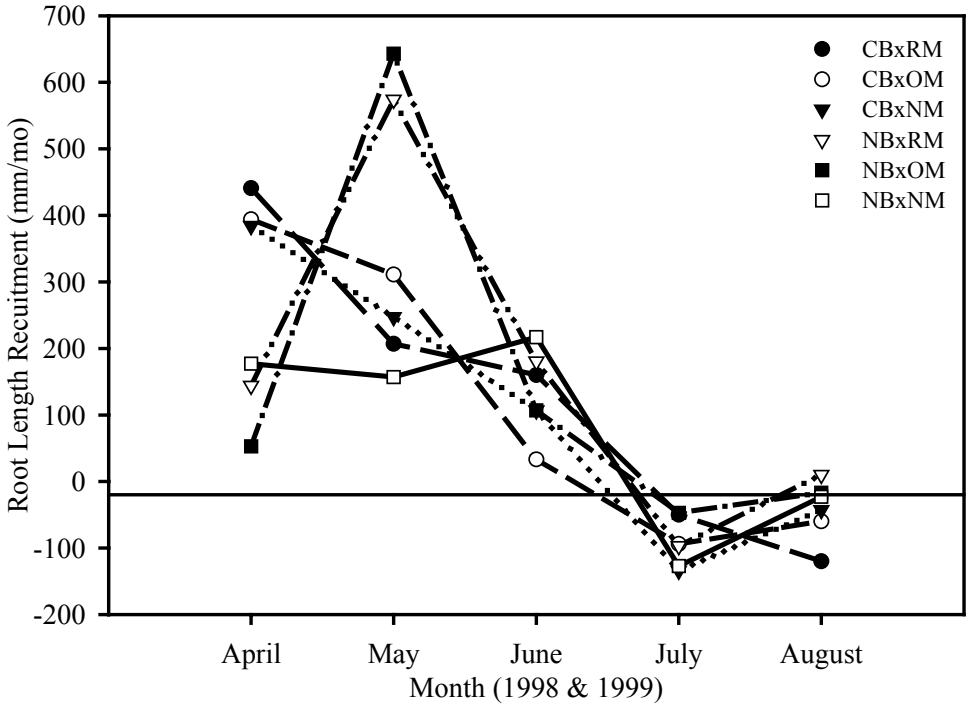

FIG. 16. Interactive effects of spring burning X mowing on root length recruitment (production – mortality). Seasonal recruitment totals for all burned plots, unburned X mown plots, and unburned X unmown controls were 491, 750, 219 mm/ season, respectively. Root length (mm) is totaled over the viewable area of 0-30 cm depth of minirhizotron (5189 mm^2). CB = cool season burn, NB = non-burned controls, RM = repeatedly mown, OM = once mown, NM = non-mown controls. Detailed statistical results are provided in Appendix I, tables A24-A25.

(burned X unmown vs. unburned X unmown) and mowing (mown once X unburned, mown repeatedly X unburned, unmown X unburned) as if two separate experiments had been conducted. The single factor analysis for spring burning revealed a total season ("between subjects") stimulation of root length recruitment on burned plots that tracked the burning response for the full factorial (Figure 16; Table A30). The single factor analysis for mowing detected a total season ("between subjects") increase in root length recruitment following the initial (April) treatment for both once mown and repeatedly mown plots in the fashion of mown X unburned plots in the full factorial (Figure 16; Table A31).

There were no interactions or main effects for existing root length (Table A32). Existing root length increased linearly until June, and then leveled off for the remainder of the growing season.

Plots burned in autumn (October 1998) were analyzed for 1999 and compared With spring burned plots and unburned controls for that treatment year only. Root length mortality and existing root length were statistically comparable on autumn burned, spring burned, and control plots in 1999 (Tables A34, A36). However, autumn burning increased total season ("between subjects") root length production (Table A33) and root length recruitment (Table A35) by 40% and 78%, respectively, relative to unburned plots during the 1999-growing season (Figures 17a,b).

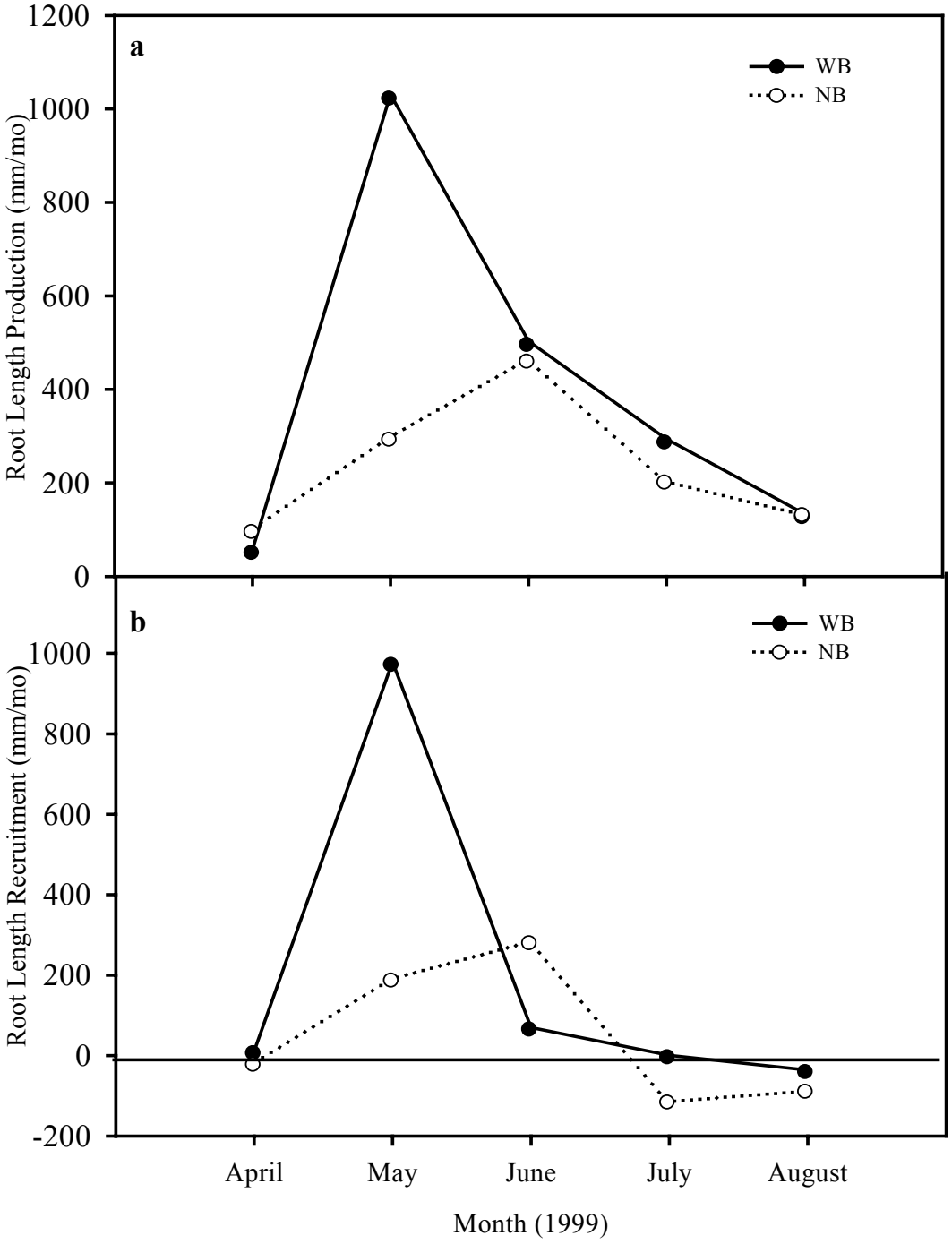

FIG. 17. Effects of autumn burning (October 1998) on average (a) root length production, and (b) root length recruitment during the 1999 growing season. Autumn burning affected seasonal values ("between subjects") for both parameters ($P = 0.0453$, $P = 0.0260$, respectively). Seasonal root production and recruitment (mm) for autumn burned plots were 2019 and 987, whereas totals for unburned controls were 1214 and 221, respectively. WB = warm season (autumn) burn, NB = non-burned controls. Detailed statistical results are provided in Appendix I, tables A29, A31).

Root ingrowth cores

Treatment year (1998 vs. 1999) significantly affected total season biomass and root length density of roots recovered from ingrowth cores (Tables A37-A38). There were no other significant interactions or main effects for root biomass or root length density from ingrowth cores (Tables A37-A40). Root biomass and root length density in 1999 were three times greater than during the 1998 drought (Figure 18).

There were no significant correlations between monthly new root area (cm/cm^2) measured from minirhizotrons and the ingrowth core metrics root length density (cm/cm^3; $R^2 = 0.019$, $P = 0.67$) and biomass production (g/m^2 to 30 cm depth; $R^2 = 0.006$, $P = 0.89$). Qualitative field observations suggest that soil moisture was greater in ingrowth soil mixtures than in the adjacent soil profile.

Discussion

Methodological differences

This study indicates that the varied responses of root systems to defoliation reported in the literature (Milchunas and Lauenroth 1993, McNaughton 1998) may be partially the result of methodological differences. With sequential coring (Böhm 1979), minirhizotrons and ingrowth techniques are among the most widely employed root sampling techniques (Vogt and Persson 1990). Results from minirhizotrons suggest that fire and mowing are dictating root dynamics independent of climate, whereas ingrowth cores indicated roots are responding to climate (precipitation) and not to burning and defoliation. In light of these divergent results, it was not surprising that measures of

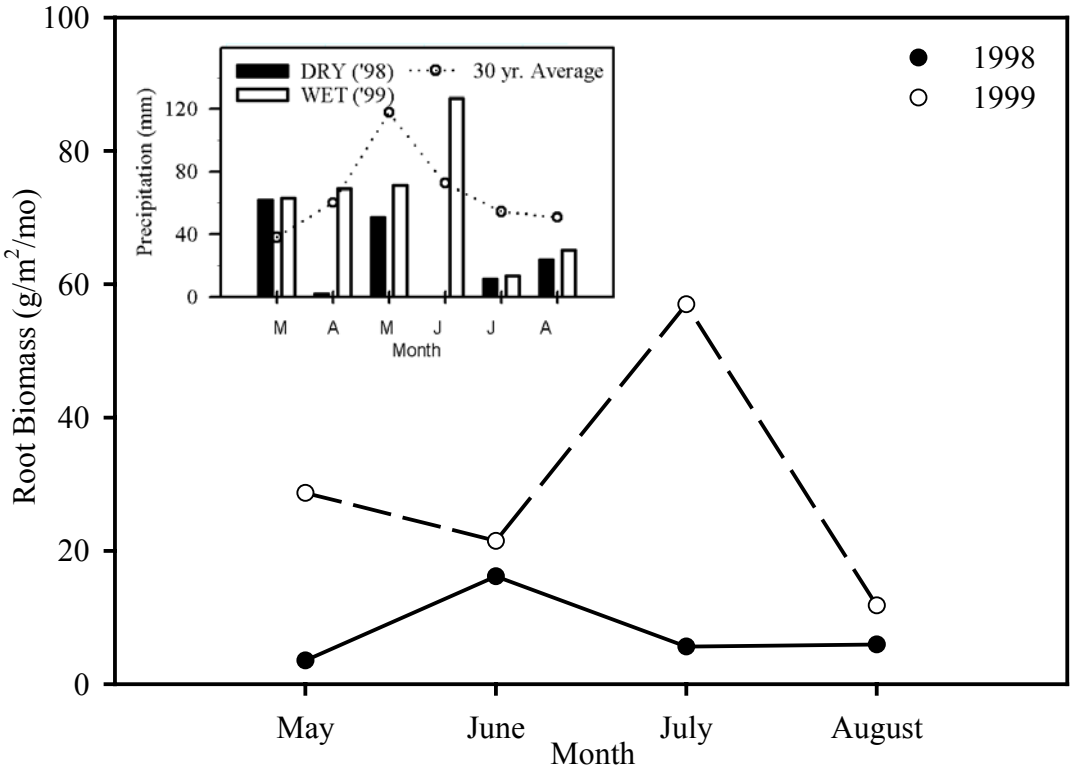

FIG 18. Effects of treatment year on root biomass recovered from ingrowth cores (root length density similar). Biomass was significantly lower over the 1998 growing season (7.9 g/m^2; "between subjects") than 1999 (24.0 g/m^2); $P < 0.0001$). 1998 coincided with an extreme drought, whereas 1999 had near normal precipitation (inset). Detailed statistical results are provided in Appendix I, tables A33-A34.

production for each technique were not correlated. Which method provides the best or the correct assessment of root growth? There is no definitive answer. Ingrowth coring imposes a highly artificial edaphic environment for root growth, as soils (both within and surrounding the core) are considerably modified. The sampling frequency (monthly) in this experimental design likely exacerbated disturbance effects. As such, the root length/biomass data from ingrowth cores cannot be considered absolutely, but rather are at best a 'relative index' for comparisons across treatments. Furthermore, they likely indicate the ability of species neighboring the core site to exploit a root-free soil rather than inherent root growth properties *per se*. (Oliveira et al. 2000).

Minirhizotrons also introduce a number of biases. Installing minirhizotrons disturbs the surrounding soil (Caldwell and Virgina 1989), potentially introduces light and temperature differences into the soil profile (Levan et al. 1987, McMichael and Taylor 1987), and may favor root "tracking" along tube surfaces (Upchurch and Ritchie 1983, Heerman and Juma 1993). However, precautions taken during installation and sampling can greatly minimize these biases (Caldwell and Virginia 1989, Smit et al. 2000, Box 2002). Minirhizotrons can track both root growth and mortality, allowing net recruitment rates to be measured (Smit et al. 2000). Qualitatively, minirhizotrons appear better suited for detecting changes in root system dynamics. In any case, results from this study caution against comparing treatment effects across root sampling techniques.

Fire, grazing, and roots

For the reasons described in the section above, interpretations of root responses

to defoliation will focus on the minirhizotron technique. Minirhizotron results indicate that fire and mowing interact to drive seasonal rates of root recruitment. Burning produced a surge in root recruitment, as did mowing in the absence of burning. However, subsequent mowing on burned plots did not further stimulate root recruitment, suggesting the two effects are not additive. Similarly, repeated mowing on both unburned and burned plots had no recurring effect following the initial increase in root length recruitment. This response suggests that the fire and mowing interaction was a function of the relative timing of defoliation (fire or mowing) events.

However, the results of the analysis of root length production and root length mortality provide compelling evidence that fire and mowing interact by affecting different components of root length recruitment. Burning in either season resulted in a dramatic (though short-lived) increase in root length production, whereas mowing had no effect on root length production. Conversely, mowing greatly minimized root mortality (again, short-lived), whereas burning had little effect. Therefore, fire and mowing did not interact to drive root production *or* root mortality, but the contrasting impacts of the main effects contributed to a critical fire and mowing interaction on root recruitment (= net outcome of root production *and* mortality). The singular and distinct effects of each disturbance on a particular compartment of root recruitment seem counterintuitive; we would expect factors that would favor root production (fire) might also mitigate root mortality. As burning occurred while plants were dormant and mowing occurred after the growing season had commenced, differences in timing may partially explain this dichotomy. Subsequent research is needed for mechanistic

explanations of these root responses to fire and mowing.

The single-factor approach (fire or grazing) common in the literature would have produced very different results than those of the fully factorial design. Analyzing these results with two single-factor designs (burned vs. unburned plots in the absence of mowing, and mown vs. unmown plots in the absence of burning) illustrates the danger in this approach. Fire in the absence of mowing increased root length production and consequently, net root recruitment. Mowing in the absence of fire decreased root length mortality, hence net root recruitment increased. An interpretation of these single-factor results might be that burning followed by mowing would maximize recruitment. Results from the fully factorial experiment clearly demonstrate this interpretation to be incorrect.

A review of the literature reveals only a few studies that have investigated fire and grazing concurrently, and only one that has used a fully factorial design. Benning and Seastedt (1997) used such a design to investigate fire and mowing effects on tallgrass prairie root characteristics. They employed both rhizotrons and soil cores (="standing crop" root biomass) in separate studies, with results that are consistent with the current study. Root length observed on rhizotrons responded only to differences between years (presumably macroclimatic variation), though they noted that sample size limitations (n=2) likely affected results. Interestingly, results from their *in situ* technique (rhizotrons) were similar to the results for the destructive sampling technique (ingrowth cores) in this study. Consistent with the minirhizotron results in the present study, Benning and Seastedt (1997) reported a fire X mowing interaction for total root biomass (live + dead) in soil cores, such that biomass was 24% lower on unburned and unmown

plots than on any other treatment combinations, which did not differ. It is striking that the only studies to explicitly look at fire and mowing in concert documented not only an interaction between fire and mowing, but that the response was the same: burning, mowing, and their combination produced an equivalent increase in fine roots relative to undefoliated controls, and the combination of fire and grazing did not produce an additive enhancement of root recruitment.

Models of root response to defoliation

Fire and mowing had neutral (ingrowth cores) and positive (minirhizotrons) effects on root growth, consistent with the field/ecosystem model (defoliation = no sustained decrease in root growth) reviewed in the Introduction. These results do not support the traditional model, wherein root growth decreases as carbon is preferentially allocated to re-establishing shoots. Both aboveground biomass *and* root length recruitment (minirhizotrons) increased dramatically following fire in the absence of mowing, and mowing had neutral effects on aboveground production but greatly enhanced root length recruitment in the absence of burning. Perhaps the beneficial aspects of defoliation (McNaughton 1983, Hulbert 1988, Oesterheld and McNaughton 1991, Briske and Richards 1995) precluded the necessity of allocation tradeoffs. Alternatively, issues of scale may have obscured decreased root growth as predicted by the traditional model. Roots were not sampled until the month following treatment. Therefore, root growth may have diminished briefly immediately following fire or mowing, but have quickly recovered by the next sampling period, effectively concealing

any reduction in roots. By contrast, the pot experiments used to develop the traditional model (Jameson 1963) were defoliated and sampled for root growth in short order. As such, the traditional model may have been relevant over narrow spatial and temporal scales. Perhaps these models should be viewed as complementary explanations of root response to defoliation over varying scales rather than competitively. At the scale of an individual plant immediately following defoliation, root production may briefly decrease as stated in the traditional model, whereas root responses would be neutral or positive over broader spatial and temporal scales as predicted by the field/ecosystem model and demonstrated in this study.

Interactive effects of fire and mowing on whole plant productivity

When combined with aboveground data (Chapter III), these results indicate that fire and mowing interact to drive whole plant biomass dynamics, and provide insights into patch level resource allocation patterns (above- vs. belowground). Spring fire stimulated an initial pulse of root recruitment in April (primarily due to increased root production). On burned plots that were not subsequently mown, this brief increase in root recruitment was followed by dramatic increases in ANPP during summer months. Presumably, this enhanced root growth provided additional moisture and nutrients required for sustained aboveground biomass production later in the season. By contrast, burned plots that were subsequently mown, while exhibiting similar root responses to burned-only plots, did not exhibit increased ANPP. Evidently, the increased availability of soil resources provided by the enhanced root system was utilized for canopy

reestablishment following mowing, effectively offsetting consumptive losses. Mowing in the absence of burning also resulted in a brief profusion of root recruitment (primarily a function of reduced root mortality). Though this enhanced root recruitment exceeded that of burning, there was no subsequent increase in ANPP, apparently also due to offsetting effects of canopy losses to mowing. Disparate responses to fire and mowing may be due to defoliation intensity (fire>>mowing, for this study) and inherent differences (e.g., selectivity, surface litter effects, scale) between fire and mowing (Chapter III, Hulbert 1988, Hobbs et al. 1991, Blair 1997, Johnson and Matchett 2001). However, these observed responses are also likely a function of the timing of each treatment. Both fall and spring burning occurred while most plants were dormant, whereas mowing began well after (ca. six weeks) the growing season had commenced. Therefore, fires consumed primarily senescent foliage and surface litter, which typically favors subsequent plant growth (Hulbert 1988). By contrast, mowing removed substantial quantities of live foliage, photosynthetic and reproductive tissues that must be replaced to reestablish carbon gain. Contrasting the relative effects of timing, intensity, and inherent effects should be a goal of future field experimentation.

These results indicate that differences between root methodologies and critical interactions between fire and mowing have precluded generalizations regarding root response to defoliation. For infrequently disturbed southern mixed grass prairie, plants responded to defoliation by increasing root recruitment, though subsequent defoliation evidently exhausted this capacity for root growth. Competing models of root response may be more accurately viewed as representing different temporal and spatial scales.

This study emphasizes that realistic assessments of above- and belowground effects of fire and grazing in grasslands must account for interactions between these disturbances.
This study emphasizes that realistic assessments of above- and belowground effects of fire and grazing in grasslands must account for interactions between these disturbances.

CHAPTER V

EFFECTS OF FIRE AND GRAZING ON SOIL RESPIRATION, MOISTURE, AND TEMPERATURE

Introduction

Concerns over rising atmospheric CO_2 and the potential for global climate change highlight the need for quantifying the dominant C fluxes of major terrestrial ecosystems. As grasslands occupy 40% of the Earth's surface (World Resources Institute 2000), they may serve as a globally important source or sink of C (Thornley et al. 1991, Glenn et al. 1993, Bremer et al. 1998, Scurlock and Hall 1998). Soil respiration, the principal mechanism by which terrestrial soil organic C is cycled to the atmosphere (Schlesinger 1997), is composed primarily of root and microbial respiration (Johansson 1992, Norman et al. 1992, Cheng et al. 1993, Rochette et al. 1997). Temperature and precipitation are typically the primary determinants of soil respiration (Kucera and Kirkham 1971, Norman et al. 1992, Raich and Schlesinger 1992, Lloyd and Taylor 1994). However, the productivity and composition of plant communities can also have profound effects on soil respiration by determining the quantity and quality of above- and belowground organic matter inputs (Raich and Schlesinger 1992, Bingham and Stevenson 1993, Fitter et al. 1998). Grasslands are characterized by recurring disturbances such as grazing and fire that affect plant community composition and

productivity (Anderson 1990). Thus, an understanding of the role of grazing and fire effects on soil respiration is critical for accurately assessing C balances of grassland ecosystems.

There are several potential scenarios by which fire and/or grazing might stimulate or suppress soil respiration (see Bremer et al. 1998 for a detailed review). Both disturbances can increase soil temperature by removing the canopy and altering albedo (particularly in the case of fire). Grazing or burning may concomitantly conserve soil moisture as evapotranspiration may decrease following defoliation (Bremer et al. 2001), and infiltration may be promoted by reducing interception by the canopy and litter layer (Owensby et al. 1970, Savage 1980, Archer and Detling 1986). While both of these effects would favor soil respiration, they might be offset by other factors. For example, fire and/or grazing can decrease near-surface soil moisture by means of increased evaporation from exposed mineral soil or increased soil water repellency (Mallik and Rahman 1985, Bremer et al. 1998). Also, if grazing reduces the quantity of above- and/or belowground organic matter inputs, root respiration and microbial activity might diminish. However, the effects of fire and grazing on above- and belowground net primary productivity (ANPP, BNPP) and community composition are highly variable (Milchunas and Laurenroth 1993) and prevent broad generalizations. Consequently, net changes in soil respiration derived from altered ANPP and BNPP are difficult to predict reliably.

The purpose of this study was to assess if burning, simulated grazing (=mowing) and their interaction affect soil respiration in a mixed grass prairie. Given the

complexity of the potential effects that these disturbances may have on soil respiration, I hypothesized that:

1. Seasonal rates of soil respiration would respond *directly* to fire and grazing through the effects these disturbances may have on soil moisture and temperature, and *indirectly* through potential fire and grazing modifications of above-and belowground net primary production (ANPP and BNPP, respectively). Soil respiration would therefore primarily track soil moisture and temperature, with NPP of secondary importance.
2. Both direct and indirect responses of soil respiration will be driven by fire and grazing interactions (Collins and Gibson 1990).

To address these questions, I initiated a factorial field experiment in 1998, and repeated the experiment on new plots in 1999.

Methods

Chapter II provides a detailed description of the study site and experimental design.

Soil respiration (SR)

Soil respiration (SR) was quantified monthly from January 1998-August 1999 using a soil respiration chamber (LICOR-6000-09) attached to an infrared gas analyzer (LICOR-6200; LICOR Inc., Lincoln, NE) (Norman et al. 1992) calibrated daily with

CO_2 of known concentration (501 ppm). The respiration chamber was seated on PVC collars (10 cm diameter) inserted to a depth of 2.5 cm and extending 4.5 cm above ground (Norman et al. 1992, McCulley 1998). PVC collars were installed the day prior to measurement and allowed to equilibrate for at least 24 h. SR was measured mid-afternoon (ca. 1300-1600 h) and once during the night (ca. 0100-0400 h) to bracket the diel range of air/soil temperatures. PVC collars were relocated to new, randomly selected subplots during each month of the experiment (Fig. 4). Soil temperature was measured simultaneously with a temperature probe inserted 10 cm into the soil adjacent to the collar. Instantaneous measurements of SR and soil temperature were scaled to monthly rates by multiplying the daytime measurements by the number of seconds between sunrise and sunset for each month, and the nighttime measurements by the time between sunset and sunrise for a weighted monthly total.

Soil chemical and physical analyses

Soil samples (0-10 cm and 10-20 cm depth) were collected at the end of each growing season (August) and analyzed for organic carbon (SOC) and total nitrogen (TN) by combustion/gas chromatography (Carlo-Erba EA-1108 elemental analyzer, CE Elantech, Lakewood, NJ) using procedures described by Nieuwenhuize et al. (1994). Soils were sieved through a 2-mm screen to remove coarse roots, dried at 60^{o}C, and pulverized with a centrifugal mill. To express SOC and TN as mass per unit volume soil at each depth, soil bulk density (g cm^{-3}) was determined for each plot by hammering steel cores (7.8 cm diameter x 20 cm length) into the mineral soil. The cores were

excavated, carefully bagged to prevent soil loss, oven dried at 105^{o}C for five days, and weighed.

Soil moisture

Volumetric soil moisture (θ; 0-30 cm) was measured monthly in each plot using time domain reflectometry (TDR; Davis and Chudobiak 1975). TDR provides an instantaneous, nondestructive measure of soil moisture by measuring the dielectric constant (κ) of the soil (Dalton et al. 1984). Pairs of stainless steel probes (0.4763 cm diameter x 32 cm long) were permanently installed 5 cm apart to a depth of 30 cm. κ was calculated by comparing the initial and final reflection points displayed on a cable tester (Tektronix Model 1502C, Beaverton, OR) as described by Baker and Allmaras (1990). Calibration equations of Topp et al. (1980) were used to derive θ from κ_1-κ_2.

Statistical analyses/design

Multivariate analysis of variance (MANOVA) was used to analyze these data as a three-factor experiment (Fire x Grazing x Treatment Year) with repeated measures (Sokal and Rohlf 1995). Since the monthly sampling variable is inherently ordinal (i.e., ranked), orthogonal contrasts (Littell et al. 1992) were used to compare the overall trends of each treatment combination through the entire growing season. In this manner, treatment effects could be emphasized over differences merely due to within-season changes in climate. Plots mown and/or burned in 1998 were followed throughout the 1999 field season. Multiple (stepwise) regression models were developed to predict

monthly SR from corresponding abiotic (soil and air temperature, soil moisture, precipitation) and biotic variables (aboveground biomass production and root dynamic parameters).

Results

Detailed MANOVA results are provided in Appendix I, Tables A41-A52. Interannual differences in precipitation and air temperature were dramatic (Figs 1-2), as 1998 was an extreme drought, whereas 1999 had near normal precipitation and air temperatures (NOAA 1998, 1999, Texas Water Development Board 2002). A summary of growing season precipitation and air temperature for 1998 and 1999 is provided in Figure 19a. See Chapter II for a detailed review of the climatic differences between 1998 and 1999.

Environmental variables

Treatment year (1998, 1999) had significant effects on growing season ("between subjects") soil temperature and soil moisture (Tables A41-A42), such that soil temperatures were higher and soil moisture lower during the drought of 1998 as compared to near-normal 1999 (Fig. 19b-c). Spring burning and treatment year interacted to affect within season ("within subjects") soil moisture, such that soil moisture was greater on burned plots in May 1998 (24%; Fig 20a), though overall seasonal trends in soil moisture were unaffected (Table A42). There were no significant differences in soil moisture and temperature between burned and unburned plots in 1999

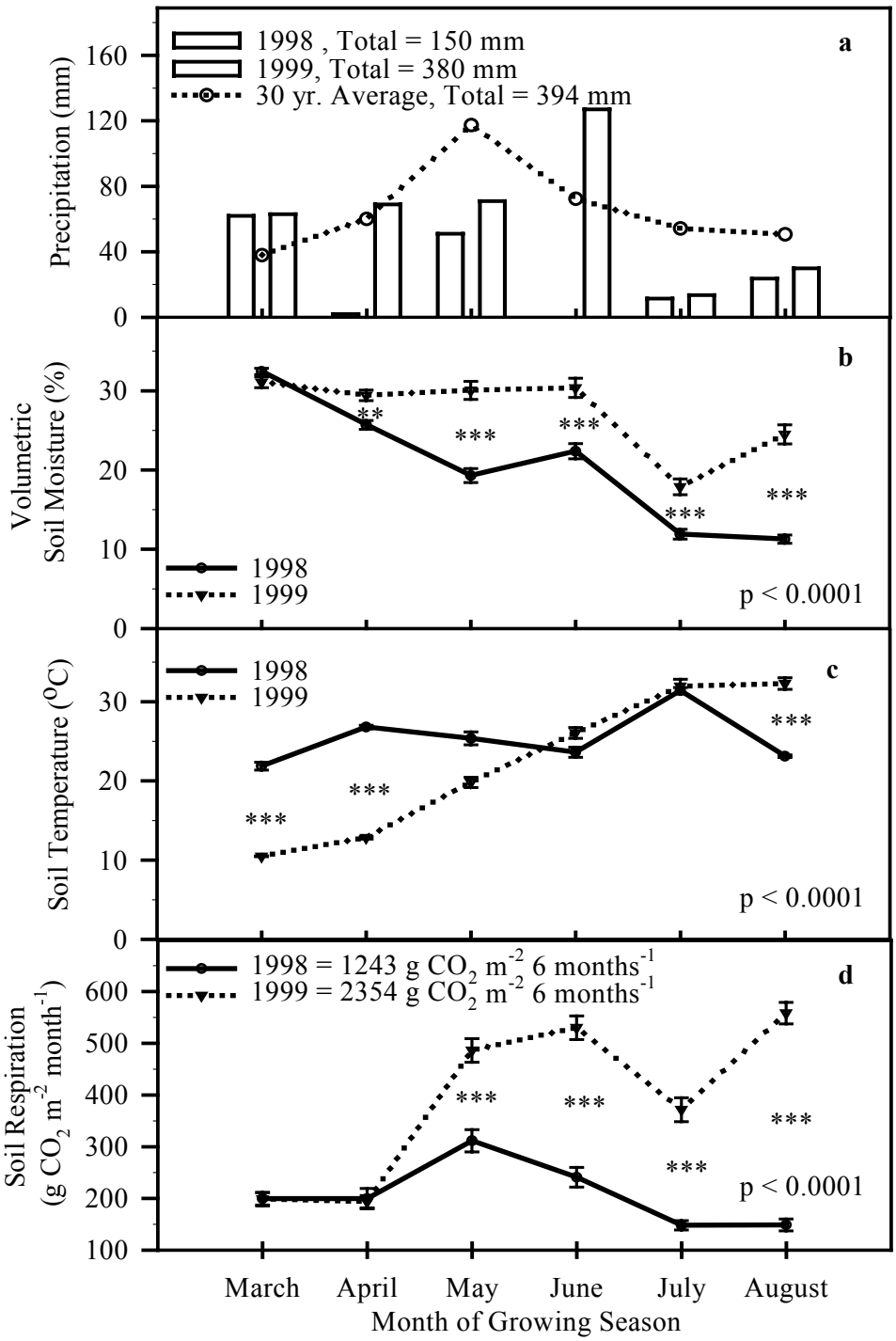

FIG. 19. Growing season (a) precipitation; (b) air temperature; (c) soil temperature (0-10cm); (d) volumetric soil moisture (0-30cm); and (e) mean daily soil respiration for 1998 and 1999. P-values denote significant overall differences between 1998 and 1999 ("between subjects"); *, **, and *** denote significant within season "within subjects") effects (P < 0.05, 0.01, and 0.001, respectively).

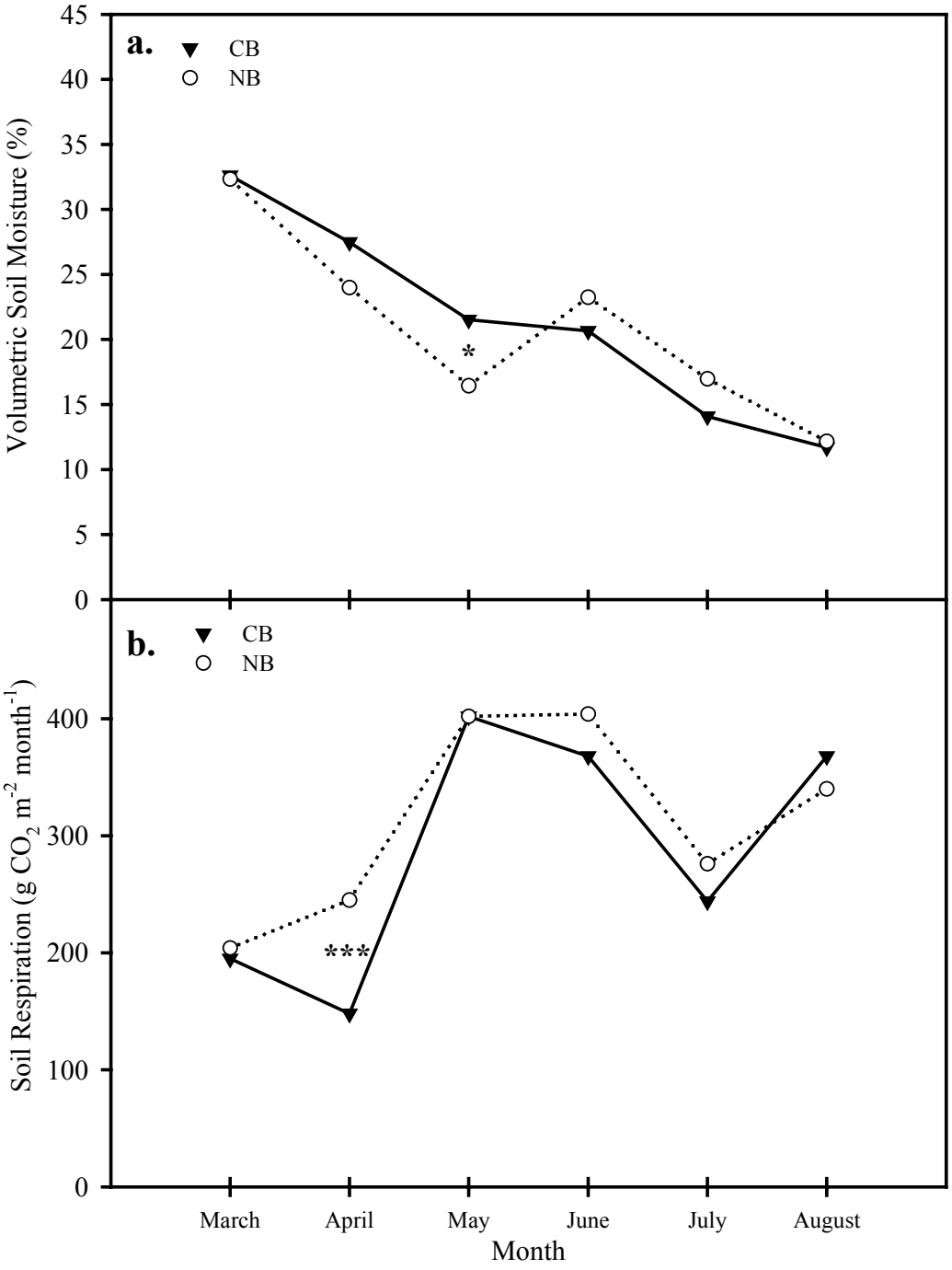

FIG. 20. Within season ("within subjects") effects of spring burning on (a) volumetric soil moisture (0-30 cm; during 1998 only), and (b) soil respiration in 1998 & 1999. Overall seasonal trends ("between subjects") were unaffected ($P > 0.05$). Detailed statistical results are presented in Appendix I, tables A37, A39. * and *** denote significant within season effects ($P < 0.05$ and $P < 0.001$, respectively).

(Table A43-44). There were no significant interactions or main effects for SOC, total N, or C:N ratio between treatments (Tables A45, A47, A49). SOC values are summarized in Table 9. Fall burning had no effect on soil C and N (Tables A46, A48, A50).

Soil respiration

Seasonal soil respiration totals are presented by treatment in Table 10. Treatment year had a significant effect on soil respiration, such that overall seasonal CO_2 flux ("between subjects") in 1999 was twice that observed in 1998 (Table A51, Fig. 19d). Regardless of treatment year, spring burning had significant within season ("within subjects") effects such that soil respiration decreased 40% on burned plots in the month following burning, then recovered to rates comparable to unburned plots as the growing season progressed (Fig. 20b). This response was ephemeral, and had no effect on overall seasonal CO_2 flux ("between subjects"; Table A51). Fall burning had no effect (Table A52) on soil respiration during the following growing season. There were no other significant interactions or main effects for soil respiration (Table A51).

As no significant overall ("between subjects") effects of fire and mowing were detected, a multiple regression model was developed for monthly SR measurements (g CO_2 m^{-2} $month^{-1}$) using data from all treatments. Monthly precipitation (mm), monthly root biomass production as measured by ingrowth cores (g/m^2; Chapter IV), and the difference between average air temperature and soil temperature (0-10 cm; ^oC) during the date of SR measurement were significant explanatory variables ($P < 0.0001$). Monthly precipitation and air temperatures explained 31% of the variance in monthly

Table 9. Soil characteristics (mean ±SE) for samples collected in August of 1998 and 1999. No treatment effects or interactions were significant ($P > 0.05$) so pooled values are presented below.

Characteristic:	**1998 (n=30/depth)**	**1999 (n=30/depth)**
Organic C (g C m^{-2}):		
0-10 cm	2712 ± 118	2948 ± 127
10-20 cm	2103 ± 119	2832 ± 296
Total N (g N m^{-2}):		
0-10 cm	281 ± 9	293 ± 11
10-20 cm	228 ± 12	310 ± 57
C:N Ratio:		
0-10 cm	9.6 ± 0.1	10.0 ± 0.1
10-20 cm	9.2 ± 0.1	10.7 ± 0.9
Soil Bulk Density (g cm^{-3}):		
0-10 cm	1.13 ± 0.02	1.14 ± 0.02
10-20 cm	1.31 ± 0.03	1.30 ± 0.03

Table 10. Seasonal (March-August) totals (mean ± S.E.) for soil CO_2 flux (g CO_2 m^{-2} 6 $months^{-1}$) by treatment. Treatment year (1998 vs. 1999) was the only significant main effect or interaction for overall seasonal trends ("between subjects"). Growing season precipitation during 1998 was only 24% normal, while 1999 was 78% of normal precipitation. See Chapter II for a detailed review of precipitation and air temperatures during the study. CB = cool season burn, WB = warm season burn, NB = non-burned, RM = repeatedly mown, OM = once mown, NM = non-mowed. Overall mean ± S.E. for 1998 = 1243±49 g CO_2 m^{-2} 6 $months^{-1}$; 1999 = 2354±60 g CO_2 m^{-2} 6 $months^{-1}$

	CBxRM	CBxOM	CBxNM	NBxRM	NBxOM	NBxNM	WBxNM
1998	1199± 134	1255± 120	1207± 80	1279± 201	1160± 35	1336± 96	n/a
1999	2011± 140	2426± 87	2303± 138	2228± 82	2585± 150	2583± 113	2218± 158

SR; adding root biomass explained only 2% more (Table 11). Soil temperature (^{o}C) at 0-10 cm soil depth, cumulative precipitation during the two weeks preceding measurement, monthly mean air temperature (^{o}C), and volumetric soil moisture (%) were also significant at the P <0.15 level, though these variables were not included in the model as they had variance inflation factors >10 (Marquardt 1970), and thus would have introduced multi-collinearity into the model (Helsel and Hirsch 1992). Monthly root length production as measured by minirhizotrons (mm; Chapter IV), and monthly aboveground live biomass (g m^{-2}; Chapter III) were non-significant explanatory variables for monthly SR (P > 0.15).

Discussion

Soil respiration is a function of abiotic factors such as soil moisture and temperature (Norman et al. 1992, Kim et al. 1992, Lloyd and Taylor 1994, Raich and Potter 1995) and biotic factors, including microbial biomass, organic matter quality, and root respiration (Kucera and Kirkham 1971, Vose et al. 1995, Luo et al. 1996). Fire and grazing can modify each of these factors in prairie ecosystems (Owensby et al. 1970, Savage 1980, Archer and Detling 1986, Knapp 1984, Briggs and Knapp 1995, Bremer et al. 1998, Knapp et al. 1998b, Johnson and Matchett 2001). However, fire and simulated grazing (=mowing) in this study had no consistent effect on soil moisture, temperature and root biomass (a proxy for root respiration) from ingrowth cores (Chapter IV). It is therefore not surprising that fire, mowing and their interaction had no effect on soil respiration. Accordingly, neither Hypotheses 1 nor 2 is supported by these results.

Table 11. Multiple regression models for monthly soil respiration (g CO_2 m^{-2} $month^{-1}$; SR). Explanatory variables are: monthly precipitation (mm; PPT), monthly average air temperature (^oC; ATEMP), difference between air temperature and soil temperature (^oC) during sampling period (DIFFTEMP), and root biomass (g/m^2) from 0-30 cm root ingrowth cores (Chapter IV; RBIO).

Model:	***F-value***	***P***	**Adj-R^2**
SR = 504.5 + 2.1(PPT) – 8.3(ATEMP)	58.9	<0.0001	0.31
SR = 260 + 2.4(PPT) + 1.1 (RBIO) – 15.0(DIFFTEMP)	24.33	<0.0001	0.33

Placing these results in the context of similar studies suggests that fire and grazing effects on soil respiration are contingent on adequate precipitation. This study was conducted during two years with below normal precipitation (Figs. 1-2; NOAA 1998, 1999, Texas Water Development Board 2002), particularly during the growing season (24% and 78% normal, respectively). Consistent with the results of this study, Bridge et al. (1983) reported that fire had no effect on soil respiration in dry eucalyptus savanna in northern Australia, and Kieft (1994) documented no microbial respiration response to grazing in semidesert grasslands and shrublands in the southwestern U.S. Conversely, researchers working in more mesic conditions have reported dramatic fire and grazing effects on soil respiration. Knapp et al. (1998b) documented increased soil respiration on annually burned and infrequently burned sites of 17% and 55% over unburned controls in tallgrass prairie, noting that rates were comparable across all treatments during periods with relatively low soil moisture. Decreased soil respiration in tallgrass prairie has also been observed following grazing or clipping (Bremer et al. 1998, Knapp et al. 1998b). Also working in tallgrass prairie, Craine et al. (1999) found increased soil respiration from soils immediately under clipped plants, whereas respiration decreased on soils adjacent to clipped plants, relative to unclipped controls. Results reported by Ansley et al. (2002) illustrate potential precipitation mediation of fire and grazing effects within a site. Working on the same experimental pasture as the present study, Ansley et al. (2002) reported increased soil CO_2 flux on burned plots during 1995, a relatively wet year (154% normal). However, consistent with results reported in the current study, Ansley et al. (2002) found that burning during a relatively

dry year (65% normal) had no effect on soil respiration. As in this study, Ansley et al. (2002) reported that mid-summer soil respiration rates were cut by more than 50% during dry vs. wet years.

Knapp et al. (1998b) attributed fire-enhancement of soil respiration to attendant increases soil temperatures on burned sites, and demonstrated that soil temperature was strongly correlated with soil respiration. This linkage between soil temperature and soil respiration has been noted by a number of authors (Whitkamp 1966, Kucera and Kirkham 1971, Lloyd and Taylor 1994, Raich and Potter 1995). However, other studies have found soil temperature to have a weak association with soil respiration (Ham et al. 1995) and root respiration (Lambers et al. 1996). Craine et al. (1999) contend that the direct impacts of soil temperature on soil respiration may be overstated at field scales. They argue that (1) soil temperature is typically correlated with other likely determinants of soil respiration (e.g., light availability), and (2) an emphasis on global scales has produced simple models of soil response that ignore ecophysiological influences that are important at local scales. Moreover, Craine et al. (1999) demonstrated that carbon availability to roots could play a predominant role (primarily via effects on root respiration) in soil CO_2 flux, whereas soil temperature relationships were inconsistent. Though root respiration was not documented in the present study, patterns of root biomass production tracked soil respiration, and soil temperature was weakly associated with soil respiration, consistent with the findings and reasoning of Craine et al. (1999). Evidence of decreased soil respiration despite documented increases in soil temperatures

following grazing or clipping (Bremer et al. 1998, Knapp et al. 1998b) further support this view.

Results from this study indicate that seasonal and interannual patterns of precipitation and air temperature are primary determinants of soil respiration in southern mixed grass prairie, in decreasing order of importance. Monthly and seasonal rates of soil CO_2 flux tracked these variables, as soil moisture, temperature, respiration, and root biomass responded similarly to drought. Potential fire and grazing effects on soil respiration in southern mixed grass prairie appear to be diffused against the influence of pronounced climatic variability.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Above- and belowground linkages

This study documents critical interactive effects of fire and simulated grazing (=mowing) on above- and belowground dynamics of southern mixed grass prairie in the Low Rolling Plains of North-Central Texas. Separate analyses of fire and mowing as independent main effects were generally consistent with numerous single-factor studies for mixed grass prairie, particularly for aboveground production. However, restricting research to single factor "fire *or* grazing" experiments does not accurately reflect the "fire *and* grazing" reality of most grasslands. Results from the single-factor analyses differed markedly from the interaction revealed by the factorial approach, emphasizing the role of composite factors in regulating functional attributes of grasslands and the perils of single- factor studies.

Burning resulted in a rapid increase in root length production and consequently, recruitment (root production – root mortality). This root recruitment supported large increases in aboveground biomass production on burned plots. Mowing in the absence of burning did not enhance root length production but did increase root length recruitment because root length mortality was dramatically decreased. This increase in root recruitment evidently supported canopy regeneration that offset consumptive losses of live foliage, as mowing effects on aboveground biomass were neutral, consistent with

many observations of grazed mixed grass prairie. However, on burned plots that were subsequently mowed to simulate livestock grazing, aboveground biomass was not enhanced, nor was there a second pulse of root recruitment.

Timing, intensity, and frequency of these defoliation events clearly contributed to this critical fire and mowing interaction, though the specific effects each disturbance had on a corresponding compartment (production or mortality) of root length recruitment suggests inherent differences in the consequences of each type of disturbance. Failure to account for fire and grazing interactions, differences in spatial and temporal scales, and methodological bias in root sampling all appear to have contributed to the widely disparate root responses to defoliation reported in the literature. For example, root biomass recovered from ingrowth cores responded only to broad scale climate patterns, in contrast to the clear fire and mowing responses observed with the minirhizotron. As such, competing models of root response to defoliation may actually be complementary, as technical and sampling artifacts confound comparisons of results.

Soil respiration, soil moisture, and soil temperature

Fire and mowing had no consistent effects on soil moisture and temperature, the primary abiotic determinants of soil respiration. It is therefore not surprising that fire and mowing had no overall effect on soil respiration, which closely tracked precipitation patterns, and to a lesser extent, air temperature and root biomass production. However, results from more mesic sites, and from the same site during an unusually wet year suggest that soil respiration can be enhanced by fire and diminished by grazing/mowing

when the constraints of severe moisture limitation are removed. Additional research is required to evaluate this moisture-dependent response, and to contrast ecophysiological and environmental determinants of soil respiration in southern mixed grass prairie.

Directions for future research

While this study has provided some insights into mixed grass prairie dynamics, it has inevitably created many more questions. Most previous work has focused on the single factor (fire *or* grazing) effects of disturbance. However, this study and others like it have demonstrated that accounting for interactions between these disturbances (fire *and* grazing) is a more realistic approach for grassland research, and that single-factor results can be misleading. Investigating potentially complex interactions between fire and grazing should therefore be a goal of grassland research.

To minimize spatial autocorrelation and potentially confounding effects of soil variability, this study was limited to small plots monitored over two growing seasons. To make inferences over broader spatio-temporal scales, the experiment (or a subset) should be replicated over larger areas grazed by animals, and monitored over longer timescales. Does a lawnmower adequately mimic a cow? Are these responses sustained as disturbance frequency increases? Do other grassland types respond similarly? At what threshold of available moisture might fire and grazing have direct consequences for soil respiration? At a more fundamental level, future research should investigate the degree to which interactive effects of fire and grazing are a function of timing,

frequency, and intensity of disturbance, and contrast these general factors with specific mechanisms and traits inherent to each type of disturbance.

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APPENDIX I

MANOVA TABLES

Table A1. Repeated measures MANOVA for monthly live aboveground biomass of all species combined. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	10.60	0.0021**
Burn	1	4.11	0.0483*
Year*Burn	1	0.26	0.6118
Mow	2	6.18	0.0041**
Year*Mow	2	1.18	0.3170
Burn*Mow	2	6.40	0.0035**
Year*Burn*Mow	2	0.75	0.4795
Tests of Within Subject Effects			
Month	3	7.10	0.0003***
Month*Year	3	0.75	0.5132
Month*Burn	3	3.69	0.0171*
Month*Year*Burn	3	1.46	0.2308
Month*Mow	6	0.88	0.5009
Month*Year*Mow	6	1.20	0.3114
Month*Burn*Mow	6	1.42	0.0349*
Month*Year*Burn*Mow	6	2.43	0.2167
Linear Contrasts for Month			
Mean	1	5.13	0.0281*
Year	1	2.03	0.1607
Burn	1	4.93	0.0313*
Year*Burn	1	0.23	0.6356
Mow	2	0.51	0.6034
Year*Mow	2	1.92	0.1582
Burn*Mow	2	2.51	0.0919
Year*Burn*Mow	2	2.48	0.0949
Quadratic Contrasts for Month			
Mean	1	2.70	0.1068
Year	1	0.13	0.7154
Burn	1	7.22	0.0099**
Year*Burn	1	3.24	0.0782
Mow	2	1.11	0.3390
Year*Mow	2	1.14	0.3295
Burn*Mow	2	0.60	0.5530
Year*Burn*Mow	2	4.09	0.0231*

Table A2. Repeated measures MANOVA for monthly standing dead aboveground biomass (all species combined). The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	1.24	0.2719
Burn	1	43.37	0.0001***
Year*Burn	1	1.53	0.2249
Mow	2	17.02	0.0001***
Year*Mow	2	0.19	0.8311
Burn*Mow	2	1.33	0.2750
Year*Burn*Mow	2	0.27	0.7671
Tests of Within Subject Effects			
Month	3	4.47	0.0003***
Month*Year	3	12.27	0.0001***
Month*Burn	3	7.60	0.0001***
Month*Year*Burn	3	1.59	0.1961
Month*Mow	6	2.07	0.0641
Month*Year*Mow	6	1.04	0.3986
Month*Burn*Mow	6	0.95	0.9569
Month*Year*Burn*Mow	6	1.03	0.9045
Linear Contrasts for Month			
Mean	1	7.90	0.0072**
Year	1	24.91	0.0001***
Burn	1	9.62	0.0033**
Year*Burn	1	2.08	0.1561
Mow	2	4.72	0.0135*
Year*Mow	2	2.10	0.1333
Burn*Mow	2	1.04	0.3606
Year*Burn*Mow	2	0.02	0.9843
Quadratic Contrasts for Month			
Mean	1	2.33	0.1339
Year	1	2.81	0.1005
Burn	1	4.03	0.0505
Year*Burn	1	0.03	0.8637
Mow	2	2.07	0.1370
Year*Mow	2	0.19	0.8309
Burn*Mow	2	1.33	0.2741
Year*Burn*Mow	2	0.62	0.5415

Table A3. Repeated measures MANOVA for monthly live aboveground biomass for all species combined (1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (March, April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	2.41	0.1321
Tests of Within Subject Effects			
Month	5	13.82	0.0001***
Month*Burn	10	5.23	0.0018**
Linear Contrasts for Month			
Mean	1	43.59	0.0001***
Burn	2	3.28	0.0731
Quadratic Contrasts for Month			
Mean	1	85.65	0.0001***
Burn	2	11.79	0.0015**

Table A4. Repeated measures MANOVA for monthly standing dead aboveground biomass (all species combined; 1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (March, April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	6.09	0.0149*
Tests of Within Subject Effects			
Month	3	9.52	0.0007***
Month*Burn	6	2.08	0.1109
Linear Contrasts for Month			
Mean	1	28.71	0.0002***
Burn	2	0.08	0.9213
Quadratic Contrasts for Month			
Mean	1	0.79	0.3920
Burn	2	0.58	0.5731

Table A5. ANOVA for ANPP (all species combined) in 1998 and 1999. The factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

Source	DF	F value	p
Year	1	2.02	0.1621
Burn	1	5.31	0.0256*
Graze	2	7.38	0.0016**
Year*Burn	1	0.00	0.9605
Year*Graze	2	1.53	0.2266
Burn*Graze	2	6.49	0.0032**
Year*Burn*Graze	2	1.05	0.3594

Table A6. ANOVA for ANPP (all species combined) in 1999. The factors are: Burn = cool season prescribed fire (cool season burn, warm season burn, control). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

Source	DF	F value	p
Burn	2	3.86	0.0508

Table A7. Repeated measures MANOVA for monthly live aboveground biomass of forb species. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	0.09	0.7714
Burn	1	3.01	0.0894
Year*Burn	1	0.85	0.3606
Mow	2	8.17	0.0009***
Year*Mow	2	0.53	0.5946
Burn*Mow	2	5.14	0.0095**
Year*Burn*Mow	2	0.99	0.3806
Tests of Within Subject Effects			
Month	3	6.52	0.0011**
Month*Year	3	0.55	0.6122
Month*Burn	3	3.03	0.0427*
Month*Year*Burn	3	3.22	0.0350*
Month*Mow	6	1.41	0.2274
Month*Year*Mow	6	2.04	0.0815
Month*Burn*Mow	6	0.78	0.5602
Month*Year*Burn*Mow	6	3.71	0.0042**
Linear Contrasts for Month			
Mean	1	17.13	0.0001***
Year	1	0.10	0.7538
Burn	1	1.41	0.2401
Year*Burn	1	0.03	0.8713
Mow	2	3.75	0.0306
Year*Mow	2	1.79	0.1785
Burn*Mow	2	2.22	0.1196
Year*Burn*Mow	2	1.51	0.2303
Quadratic Contrasts for Month			
Mean	1	3.02	0.0887
Year	1	0.86	0.3589
Burn	1	0.77	0.3857
Year*Burn	1	2.93	0.0935
Mow	2	0.29	0.7511
Year*Mow	2	1.72	0.1905
Burn*Mow	2	0.27	0.7649
Year*Burn*Mow	2	3.75	0.0308*

Table A8. Repeated measures MANOVA for monthly live *Bromus japonicus* aboveground biomass. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	5.94	0.0186*
Burn	1	13.75	0.0006***
Year*Burn	1	0.08	0.7722
Mow	2	1.24	0.2995
Year*Mow	2	0.14	0.8655
Burn*Mow	2	0.70	0.5017
Year*Burn*Mow	2	1.56	0.2199
Tests of Within Subject Effects			
Month	3	29.56	0.0001***
Month*Year	3	1.60	0.2100
Month*Burn	3	10.39	0.0002***
Month*Year*Burn	3	0.51	0.5779
Month*Mow	6	0.27	0.8732
Month*Year*Mow	6	0.86	0.4762
Month*Burn*Mow	6	1.47	0.2235
Month*Year*Burn*Mow	6	1.47	0.2234
Linear Contrasts for Month			
Mean	1	94.85	0.0001***
Year	1	5.80	0.0200*
Burn	1	33.10	0.0001***
Year*Burn	1	0.40	0.5280
Mow	2	0.24	0.7843
Year*Mow	2	0.29	0.7495
Burn*Mow	2	3.64	0.0339*
Year*Burn*Mow	2	2.90	0.0646
Quadratic Contrasts for Month			
Mean	1	17.76	0.0001***
Year	1	0.22	0.6445
Burn	1	7.01	0.0110*
Year*Burn	1	0.18	0.6766
Mow	2	0.36	0.7009
Year*Mow	2	0.13	0.8770
Burn*Mow	2	1.15	0.3256
Year*Burn*Mow	2	2.02	0.1445

Table A9. Repeated measures MANOVA for monthly live *Nasella leucotricha* aboveground biomass. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	3.97	0.0522
Burn	1	3.30	0.0759
Year*Burn	1	0.26	0.6123
Mow	2	0.70	0.5016
Year*Mow	2	0.88	0.4218
Burn*Mow	2	0.63	0.5359
Year*Burn*Mow	2	0.19	0.8243
Tests of Within Subject Effects			
Month	3	10.39	0.0001***
Month*Year	3	2.02	0.1399
Month*Burn	3	0.81	0.4421
Month*Year*Burn	3	2.02	0.1406
Month*Mow	6	0.90	0.4669
Month*Year*Mow	6	0.67	0.6082
Month*Burn*Mow	6	1.13	0.3448
Month*Year*Burn*Mow	6	0.30	0.8714
Linear Contrasts for Month			
Mean	1	1.20	0.2790
Year	1	1.25	0.2691
Burn	1	0.06	0.8024
Year*Burn	1	0.41	0.5242
Mow	2	2.00	0.1472
Year*Mow	2	0.72	0.4933
Burn*Mow	2	0.19	0.8289
Year*Burn*Mow	2	0.48	0.6220
Quadratic Contrasts for Month			
Mean	1	2.66	0.1098
Year	1	4.68	0.0356*
Burn	1	1.78	0.1888
Year*Burn	1	2.41	0.1272
Mow	2	0.06	0.9378
Year*Mow	2	0.19	0.8237
Burn*Mow	2	1.79	0.1784
Year*Burn*Mow	2	0.24	0.7873

Table A10. Repeated measures MANOVA for monthly live *Bouteloua curtipendula* aboveground biomass. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	0.80	0.3762
Burn	1	2.69	0.1016
Year*Burn	1	0.31	0.5790
Mow	2	1.27	0.2910
Year*Mow	2	0.10	0.9007
Burn*Mow	2	0.63	0.5351
Year*Burn*Mow	2	1.16	0.3211
Tests of Within Subject Effects			
Month	3	3.61	0.0250*
Month*Year	3	1.03	0.3679
Month*Burn	3	7.04	0.0008***
Month*Year*Burn	3	0.41	0.6941
Month*Mow	6	1.36	0.2501
Month*Year*Mow	6	1.85	0.1146
Month*Burn*Mow	6	0.97	0.4361
Month*Year*Burn*Mow	6	1.38	0.2414
Linear Contrasts for Month			
Mean	1	10.87	0.0019**
Year	1	0.03	0.8633
Burn	1	1.45	0.2342
Year*Burn	1	0.16	0.6898
Mow	2	4.09	0.0230*
Year*Mow	2	0.76	0.4718
Burn*Mow	2	0.10	0.9021
Year*Burn*Mow	2	3.39	0.0422*
Quadratic Contrasts for Month			
Mean	1	1.89	0.1761
Year	1	3.73	0.0596
Burn	1	14.90	0.0003***
Year*Burn	1	1.29	0.2624
Mow	2	1.20	0.3089
Year*Mow	2	1.38	0.2627
Burn*Mow	2	1.99	0.1484
Year*Burn*Mow	2	0.10	0.9021

Table A11. Repeated measures MANOVA for monthly live aboveground biomass of all C4 grasses other than *Bouteloua curtipendula*. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	1.47	0.2307
Burn	1	0.06	0.8131
Year*Burn	1	0.61	0.4384
Mow	2	0.33	0.7217
Year*Mow	2	1.54	0.2246
Burn*Mow	2	0.16	0.8562
Year*Burn*Mow	2	2.68	0.0791
Tests of Within Subject Effects			
Month	3	1.93	0.1496
Month*Year	3	0.60	0.5532
Month*Burn	3	0.40	0.6800
Month*Year*Burn	3	1.20	0.3058
Month*Mow	6	0.82	0.5169
Month*Year*Mow	6	1.28	0.2812
Month*Burn*Mow	6	1.54	0.1940
Month*Year*Burn*Mow	6	0.44	0.7840
Linear Contrasts for Month			
Mean	1	4.55	0.0380*
Year	1	1.51	0.2244
Burn	1	0.64	0.4282
Year*Burn	1	2.86	0.0972
Mow	2	0.28	0.7608
Year*Mow	2	2.00	0.1463
Burn*Mow	2	1.86	0.1660
Year*Burn*Mow	2	0.19	0.8304
Quadratic Contrasts for Month			
Mean	1	1.32	0.2556
Year	1	0.05	0.8290
Burn	1	0.05	0.8308
Year*Burn	1	0.27	0.6066
Mow	2	1.94	0.1551
Year*Mow	2	2.65	0.0808
Burn*Mow	2	1.04	0.3617
Year*Burn*Mow	2	0.80	0.4566

Table A12. Repeated measures MANOVA for monthly live forb aboveground biomass (1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (March, April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	1.15	0.3496
Tests of Within Subject Effects			
Month	5	6.93	0.0015**
Month*Burn	10	3.14	0.0190*
Linear Contrasts for Month			
Mean	1	10.96	0.0062**
Burn	2	1.51	0.2608
Quadratic Contrasts for Month			
Mean	1	6.57	0.0249*
Burn	2	5.0	0.0263*

Table A13. Repeated measures MANOVA for monthly live *Bromus japonicus* aboveground biomass (1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (March, April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	0.50	0.6176
Tests of Within Subject Effects			
Month	5	5.13	0.0160*
Month*Burn	10	1.46	0.2487
Linear Contrasts for Month			
Mean	1	2.63	0.1309
Burn	2	3.62	0.0587
Quadratic Contrasts for Month			
Mean	1	20.00	0.0008***
Burn	2	2.04	0.1723

Table A14. Repeated measures MANOVA for monthly live *Nasella leucotricha* aboveground biomass (1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (March, April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	1.44	0.2743
Tests of Within Subject Effects			
Month	5	2.94	0.0755
Month*Burn	10	1.34	0.2844
Linear Contrasts for Month			
Mean	1	4.14	0.0646
Burn	2	1.95	0.1854
Quadratic Contrasts for Month			
Mean	1	8.84	0.0116*
Burn	2	2.14	0.1599

Table A15. Repeated measures MANOVA for monthly live *Bouteluoa curtipendula* aboveground biomass (1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (March, April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	1.51	0.2610
Tests of Within Subject Effects			
Month	5	0.81	0.4379
Month*Burn	10	1.03	0.4065
Linear Contrasts for Month			
Mean	1	5.37	0.0390*
Burn	2	1.01	0.3926
Quadratic Contrasts for Month			
Mean	1	0.26	0.6226
Burn	2	2.26	0.1474

Table A16. Repeated measures MANOVA for monthly live aboveground biomass for all C4 grasses other than *Bouteluoa curtipendula* (1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	0.78	0.4818
Tests of Within Subject Effects			
Month	5	2.62	0.0904
Month*Burn	10	1.42	0.2562
Linear Contrasts for Month			
Mean	1	12.72	0.0039**
Burn	2	1.15	0.3490
Quadratic Contrasts for Month			
Mean	1	0.03	0.8607
Burn	2	0.35	0.7098

Table A17. Repeated measures MANOVA for monthly aboveground biomass (all species combined) for cool season burning in the absence of mowing in 1998 and 1999. The factors are: Burn = prescribed fire (cool season, control), Year = year of treatment (1998, 1999), and Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	1.50	0.2388
Burn	1	10.12	0.0058**
Tests of Within Subject Effects			
Year*Burn	1	0.04	0.8401
Month	3	2.25	0.1176
Month*Year	3	0.05	0.9543
Month*Burn	3	1.88	0.1658
Month*Year*Burn	3	2.76	0.0748
Linear Contrasts for Month			
Mean	1	1.73	0.2064
Year	1	0.01	0.9192
Burn	1	2.92	0.1070
Quadratic Contrasts for Month			
Year*Burn	1	6.77	0.0193*
Quadratic Contrasts for Month			
Mean	1	1.29	0.2720
Year	1	0.00	0.9490
Burn	1	1.82	0.1958
Year*Burn	1	2.24	0.1544

Table A18. Repeated measures MANOVA for monthly live aboveground biomass (all species combined) for mowing in the absence of burning in 1998 and 1999. The factors are: Mowing = simulated grazing treatment (repeatedly mown, once mown, control), Year = year of treatment (1998, 1999), and Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	1.04	0.3172
Mow	2	0.17	0.8444
Tests of Within Subject Effects			
Year*Mow	2	0.26	0.7748
Month	3	3.57	0.0267*
Month*Year	3	0.43	0.6940
Month*Mow	6	0.35	0.8778
Month*Year*Mow	6	0.94	0.4626
Linear Contrasts for Month			
Mean	1	0.30	0.5859
Year	1	1.48	0.2357
Mow	1	0.37	0.6922
Quadratic Contrasts for Month			
Year*Mow	1	0.63	0.5420
Mean	1	3.4	0.0739
Year	1	0.18	0.6744
Mow	1	0.87	0.4311
Year*Mow	1	2.63	0.0929

Table A19. Repeated measures MANOVA for the proportion of C_3 aboveground biomass to the total aboveground biomass (all plants). Data are arcsine transformed. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	1.15	0.2892
Burn	1	2.00	0.1639
Year*Burn	1	0.32	0.5756
Mow	2	6.21	0.0041**
Year*Mow	2	1.22	0.3045
Burn*Mow	2	0.23	0.7978
Year*Burn*Mow	2	0.96	0.3888
Tests of Within Subject Effects			
Month	3	10.50	0.0001***
Month*Year	3	1.04	0.3704
Month*Burn	3	0.97	0.3997
Month*Year*Burn	3	1.71	0.1772
Month*Mow	6	2.50	0.0346*
Month*Year*Mow	6	1.65	0.1090
Month*Burn*Mow	6	1.45	0.2043
Month*Year*Burn*Mow	6	1.73	0.4342
Linear Contrasts for Month			
Mean	1	29.11	0.0001***
Year	1	1.15	0.2901
Burn	1	0.44	0.5084
Year*Burn	1	2.46	0.1238
Mow	2	0.58	0.5632
Year*Mow	2	0.56	0.5753
Burn*Mow	2	1.05	0.3572
Year*Burn*Mow	2	1.89	0.1634
Quadratic Contrasts for Month			
Mean	1	1.57	0.2160
Year	1	0.00	0.9539
Burn	1	0.52	0.4736
Year*Burn	1	0.80	0.3756
Mow	2	4.56	0.0158*
Year*Mow	2	0.55	0.5828
Burn*Mow	2	4.08	0.0236*
Year*Burn*Mow	2	2.79	0.0724

Table A20. Repeated measures MANOVA for the proportion of C_3 grass biomass to the total aboveground grass biomass. Data are arcsine transformed. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	2.40	0.1324
Burn	1	0.01	0.9123
Year*Burn	1	1.48	0.2329
Mow	2	1.06	0.3599
Year*Mow	2	1.03	0.3694
Burn*Mow	2	0.97	0.3893
Year*Burn*Mow	2	0.85	0.4393
Tests of Within Subject Effects			
Month	3	8.47	0.0004***
Month*Year	3	0.60	0.5603
Month*Burn	3	0.55	0.5882
Month*Year*Burn	3	0.41	0.6762
Month*Mow	6	0.96	0.4422
Month*Year*Mow	6	1.56	0.1926
Month*Burn*Mow	6	2.02	0.0991
Month*Year*Burn*Mow	6	1.06	0.3848
Linear Contrasts for Month			
Mean	1	14.79	0.0006**
Year	1	1.38	0.2498
Burn	1	0.35	0.5583
Year*Burn	1	0.52	0.4786
Mow	2	0.08	0.9263
Year*Mow	2	0.84	0.4433
Burn*Mow	2	0.95	0.3994
Year*Burn*Mow	2	0.30	0.7416
Quadratic Contrasts for Month			
Mean	1	9.92	0.0038**
Year	1	0.02	0.8943
Burn	1	0.05	0.8233
Year*Burn	1	0.57	0.4562
Mow	2	1.15	0.3318
Year*Mow	2	0.18	0.8376
Burn*Mow	2	4.44	0.0208*
Year*Burn*Mow	2	0.76	0.4788

Table A21. Repeated measures MANOVA for $\delta^{13}C$ of roots recovered from ingrowth cores. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	1.12	0.3017
Burn	1	0.09	0.7670
Year*Burn	1	1.24	0.2772
Mow	2	0.33	0.7194
Year*Mow	2	0.97	0.3956
Burn*Mow	2	1.72	0.2035
Year*Burn*Mow	2	1.25	0.3078
Tests of Within Subject Effects			
Month	2	13.02	0.0001***
Month*Year	2	1.92	0.1682
Month*Burn	2	3.09	0.0608
Month*Year*Burn	2	0.49	0.6028
Month*Mow	4	0.73	0.5655
Month*Year*Mow	4	1.71	0.1708
Month*Burn*Mow	4	1.02	0.4052
Month*Year*Burn*Mow	4	1.85	0.1434
Linear Contrasts for Month			
Mean	1	22.10	0.0001**
Year	1	0.66	0.4246
Burn	1	3.46	0.0767
Year*Burn	1	0.43	0.5176
Mow	2	0.46	0.6365
Year*Mow	2	2.70	0.0905
Burn*Mow	2	0.54	0.5909
Year*Burn*Mow	2	1.40	0.2682
Quadratic Contrasts for Month			
Mean	1	1.49	0.2362
Year	1	7.72	0.0113*
Burn	1	2.61	0.1214
Year*Burn	1	0.56	0.4637
Mow	2	1.08	0.3590
Year*Mow	2	0.46	0.6377
Burn*Mow	2	1.63	0.2197
Year*Burn*Mow	2	2.42	0.1133

Table A22. Repeated measures MANOVA for the proportion of C_3 aboveground biomass to the total aboveground biomass (all plants; 1999 only). Data are arcsine transformed. The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	3.99	0.0468*
Tests of Within Subject Effects			
Month	3	5.43	0.0131*
Month*Burn	6	1.86	0.1549
Linear Contrasts for Month			
Mean	1	18.03	0.0011**
Burn	2	1.28	0.3124
Quadratic Contrasts for Month			
Mean	1	0.35	0.5634
Burn	2	2.27	0.1461

Table A23. Repeated measures MANOVA for the proportion of C_3 grass biomass to the total aboveground grass biomass (1999 only). Data are arcsine transformed. The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month.

Source	DF	F value	p
Burn	2	2.34	0.1523
Tests of Within Subject Effects			
Month	3	3.21	0.0764
Month*Burn	6	0.64	0.6167
Linear Contrasts for Month			
Mean	1	7.70	0.0216*
Burn	2	0.38	0.6966
Quadratic Contrasts for Month			
Mean	1	3.68	0.0874
Burn	2	0.75	0.4992

Table A24. Repeated measures MANOVA for $\delta^{13}C$ of roots recovered from ingrowth cores (1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (May, June, July). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	0.27	0.7672*
Tests of Within Subject Effects			
Month	2	11.92	0.0017**
Month*Burn	4	2.79	0.0780
Linear Contrasts for Month			
Mean	1	9.54	0.0149*
Burn	2	0.94	0.4282
Quadratic Contrasts for Month			
Mean	1	17.19	0.0032**
Burn	2	6.90	0.0182

Table A25. Repeated measures MANOVA for $\delta^{13}C$ of soils collected in August of 1998, 1999. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Depth = soil depth (0-10 cm, 10-20 cm). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

Source	DF	F value	p
Year	1	0.45	0.5064
Burn	1	2.13	0.1528
Year*Burn	1	1.54	0.2229
Mow	2	1.40	0.2609
Year*Mow	2	0.68	0.5112
Burn*Mow	2	0.09	0.9115
Year*Burn*Mow	2	0.96	0.3907
Tests of Within Subject Effects			
Depth	1	201.91	0.0001***
Depth*Year	1	2.75	0.1062
Depth*Burn	1	3.69	0.0626
Depth*Year*Burn	1	0.05	0.8250
Depth*Mow	2	0.49	0.6142
Depth*Year*Mow	2	0.29	0.7516
Depth*Burn*Mow	2	0.22	0.8053
Depth*Year*Burn*Mow	2	0.41	0.6660

Table A26. Repeated measures MANOVA for $\delta^{13}C$ of soils collected in August 1999. The two factors are: Burn = prescribed fire (warm season, cool season, control), Depth = soil depth (0-10 cm, 10-20 cm). Because the addition of warm season plots unbalanced the design, only samples from unmown plots were used in the analysis. Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

Source	DF	F value	p
Burn	2	0.21	0.8156
Tests of Within Subject Effects			
Depth	1	67.32	0.0001**
Depth*Burn	2	0.38	0.6911

Table A27. Repeated measures MANOVA for root length production (log transformed) from minirhizotron images. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	1.44	0.2395
Burn	1	0.14	0.7115
Year*Burn	1	0.68	0.4170
Mow	2	0.85	0.4382
Year*Mow	2	0.92	0.4076
Burn*Mow	2	1.30	0.2864
Year*Burn*Mow	2	0.70	0.5040
Tests of Within Subject Effects			
Month	3	14.37	0.0001***
Month*Year	3	1.69	0.1875
Month*Burn	3	3.18	0.0409*
Month*Year*Burn	3	0.52	0.6190
Month*Mow	6	2.04	0.0833
Month*Year*Mow	6	1.45	0.2205
Month*Burn*Mow	6	0.81	0.5360
Month*Year*Burn*Mow	6	0.25	0.9280
Linear Contrasts for Month			
Mean	1	1.60	0.2145
Year	1	0.00	0.9954
Burn	1	5.49	0.0253*
Year*Burn	1	0.23	0.6375
Mow	2	3.45	0.0435*
Year*Mow	2	0.69	0.5095
Burn*Mow	2	0.18	0.8327
Year*Burn*Mow	2	0.27	0.7648
Quadratic Contrasts for Month			
Mean	1	33.12	0.0001***
Year	1	4.58	0.0398*
Burn	1	2.20	0.1473
Year*Burn	1	1.12	0.2970
Mow	2	5.70	0.0074**
Year*Mow	2	3.57	0.0396*
Burn*Mow	2	0.92	0.4096
Year*Burn*Mow	2	0.08	0.9199

Table A28. Repeated measures MANOVA for root length mortality (log transformed) from minirhizotron images. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	1.49	0.2315
Burn	1	0.01	0.9408
Year*Burn	1	1.71	0.2001
Mow	2	1.34	0.2772
Year*Mow	2	0.19	0.8293
Burn*Mow	2	1.92	0.1643
Year*Burn*Mow	2	0.77	0.4719
Tests of Within Subject Effects			
Month	3	14.15	0.0001***
Month*Year	3	2.23	0.1058
Month*Burn	3	2.99	0.0477*
Month*Year*Burn	3	2.35	0.0928
Month*Mow	6	3.38	0.0094**
Month*Year*Mow	6	1.23	0.3056
Month*Burn*Mow	6	0.88	0.4925
Month*Year*Burn*Mow	6	0.74	0.5921
Linear Contrasts for Month			
Mean	1	14.55	0.0006***
Year	1	0.04	0.8470
Burn	1	0.98	0.3301
Year*Burn	1	0.02	0.8761
Mow	2	2.33	0.1137
Year*Mow	2	0.70	0.5058
Burn*Mow	2	1.38	0.2661
Year*Burn*Mow	2	0.74	0.4863
Quadratic Contrasts for Month			
Mean	1	20.07	0.0011**
Year	1	1.09	0.3048
Burn	1	5.50	0.0256*
Year*Burn	1	4.78	0.0364*
Mow	2	2.18	0.1302
Year*Mow	2	1.00	0.3796
Burn*Mow	2	0.12	0.8880
Year*Burn*Mow	2	0.53	0.5961

Table A29. Repeated measures MANOVA for root length recruitment (log transformed) from minirhizotron images. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	1.23	0.2815
Burn	1	0.01	0.9269
Year*Burn	1	0.06	0.8100
Mow	2	1.83	0.1896
Year*Mow	2	0.30	0.7396
Burn*Mow	2	8.26	0.0028**
Year*Burn*Mow	2	0.30	0.4369
Tests of Within Subject Effects			
Month	3	17.09	0.0001***
Month*Year	3	1.09	0.3582
Month*Burn	3	2.08	0.1171
Month*Year*Burn	3	1.16	0.3344
Month*Mow	6	1.77	0.1274
Month*Year*Mow	6	2.21	0.0595
Month*Burn*Mow	6	0.57	0.7428
Month*Year*Burn*Mow	6	1.09	0.3797
Linear Contrasts for Month			
Mean	1	177.54	0.0001***
Year	1	1.55	0.2296
Burn	1	2.41	0.1378
Year*Burn	1	0.00	0.9897
Mow	2	1.06	0.3656
Year*Mow	2	1.49	0.2527
Burn*Mow	2	1.36	0.2818
Year*Burn*Mow	2	3.57	0.0494*
Quadratic Contrasts for Month			
Mean	1	7.16	0.0154*
Year	1	0.32	0.5793
Burn	1	1.31	0.2672
Year*Burn	1	0.97	0.3385
Mow	2	0.62	0.5470
Year*Mow	2	3.90	0.0391*
Burn*Mow	2	1.13	0.3441
Year*Burn*Mow	2	2.11	0.1505

Table A30. Repeated measures MANOVA for monthly root length recruitment for cool season burning in the absence of mowing in 1998 and 1999 (log transformed). The factors are: Burn = prescribed fire (cool season, control), Year = year of treatment (1998, 1999), and Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	21.88	0.0023**
Burn	1	7.95	0.0258*
Tests of Within Subject Effects			
Year*Burn	1	0.02	0.8887
Month	4	9.86	0.0009***
Month*Year	4	3.46	0.0481*
Month*Burn	4	0.84	0.4663
Month*Year*Burn	4	2.66	0.0910
Linear Contrasts for Month			
Year*Burn	1	4.42	0.0735
Mean	1	43.59	0.0004***
Year	1	0.28	0.6141
Burn	1	4.62	0.0735
Quadratic Contrasts for Month			
Year*Burn	1	6.52	0.0380*
Mean	1	7.11	0.0322*
Year	1	5.09	0.0586
Burn	1	0.44	0.5298

Table A31. Repeated measures MANOVA for monthly root length recruitment for mowing in the absence of burning in 1998 and 1999 (log transformed). The factors are: Mowing = simulated grazing treatment (repeatedly mown, once mown, control), Year = year of treatment (1998, 1999), and Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	0.27	0.6137
Mow	2	7.95	0.0040**
Tests of Within Subject Effects			
Year*Mow	2	0.66	0.5294
Month	3	13.99	0.0001***
Month*Year	3	0.48	0.6257
Month*Mow	6	3.04	0.0314*
Month*Year*Mow	6	1.32	0.2849
Linear Contrasts for Month			
Mean	1	46.30	0.0001***
Year	1	1.32	0.2669
Mow	1	10.35	0.0013**
Quadratic Contrasts for Month			
Year*Mow	1	2.58	0.1067
Mean	1	10.01	0.0060**
Year	1	0.24	0.6305
Mow	1	0.66	0.5287
Year*Mow	1	0.29	0.7521

Table A32. Repeated measures MANOVA for existing root length (log transformed) from minirhizotron images. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	1.53	0.2249
Burn	1	0.08	0.7839
Year*Burn	1	0.09	0.7687
Mow	2	0.77	0.4702
Year*Mow	2	0.27	0.7675
Burn*Mow	2	0.36	0.6989
Year*Burn*Mow	2	0.32	0.7281
Tests of Within Subject Effects			
Month	3	28.48	0.0001***
Month*Year	3	0.47	0.5989
Month*Burn	3	0.58	0.5393
Month*Year*Burn	3	0.03	0.9492
Month*Mow	6	2.61	0.0536
Month*Year*Mow	6	1.29	0.2877
Month*Burn*Mow	6	0.89	0.4639
Month*Year*Burn*Mow	6	0.49	0.7123
Linear Contrasts for Month			
Mean	1	32.77	0.0001***
Year	1	0.56	0.4589
Burn	1	0.10	0.7497
Year*Burn	1	0.00	0.9886
Mow	2	3.81	0.0331*
Year*Mow	2	1.75	0.1897
Burn*Mow	2	0.79	0.4614
Year*Burn*Mow	2	0.64	0.5365
Quadratic Contrasts for Month			
Mean	1	28.23	0.0001***
Year	1	0.49	0.4880
Burn	1	0.67	0.4193
Year*Burn	1	0.00	0.9574
Mow	2	1.32	0.2821
Year*Mow	2	0.03	0.9733
Burn*Mow	2	1.25	0.2993
Year*Burn*Mow	2	0.39	0.6812

Table A33. Repeated measures MANOVA for monthly root length production from minirhizotron images (log transformed) for 1999 only. The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	4.05	0.0453*
Tests of Within Subject Effects			
Month	3	11.88	0.0001***
Month*Burn	6	2.86	0.0379*
Linear Contrasts for Month			
Mean	1	12.16	0.0045**
Burn	2	2.82	0.0990
Quadratic Contrasts for Month			
Mean	1	26.66	0.0002***
Burn	2	2.12	0.1628

Table A34. Repeated measures MANOVA for monthly root length mortality from minirhizotron images (log transformed) for 1999 only. The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	0.21	0.8173
Tests of Within Subject Effects			
Month	3	4.59	0.0182*
Month*Burn	6	0.96	0.4482
Linear Contrasts for Month			
Mean	1	1.33	0.2718
Burn	2	0.80	0.4709
Quadratic Contrasts for Month			
Mean	1	9.74	0.0088**
Burn	2	0.77	0.4857

Table A35. Repeated measures MANOVA for root length recruitment from minirhizotron images (log transformed) for 1999 only. The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	5.03	0.0260*
Tests of Within Subject Effects			
Month	3	9.54	0.0023**
Month*Burn	6	2.46	0.0910
Linear Contrasts for Month			
Mean	1	29.91	0.0001***
Burn	2	3.65	0.0576
Quadratic Contrasts for Month			
Mean	1	16.18	0.0017**
Burn	2	9.29	0.0036**

Table A36. Repeated measures MANOVA for existing root length from minirhizotron images (log transformed) for 1999 only. The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Burn	2	2.81	0.0997
Tests of Within Subject Effects			
Month	3	12.86	0.0004***
Month*Burn	6	2.91	0.0526
Linear Contrasts for Month			
Mean	1	20.98	0.0006***
Burn	2	4.28	0.0395*
Quadratic Contrasts for Month			
Mean	1	3.06	0.1060
Burn	2	1.17	0.3432

Table A37. Repeated measures MANOVA for monthly root length density production from ingrowth cores (log transformed). The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Year	1	26.01	0.0001***
Burn	1	0.42	0.5218
Year*Burn	1	0.28	0.6015
Mow	2	0.76	0.4715
Year*Mow	2	0.76	0.4743
Burn*Mow	2	2.19	0.1227
Year*Burn*Mow	2	2.57	0.0872
Tests of Within Subject Effects			
Month	3	9.76	0.0001***
Month*Year	3	5.39	0.0029**
Month*Burn	3	2.02	0.1246
Month*Year*Burn	3	1.23	0.2991
Month*Mow	6	1.16	0.3331
Month*Year*Mow	6	2.16	0.0622
Month*Burn*Mow	6	1.55	0.1791
Month*Year*Burn*Mow	6	1.77	0.1228
Linear Contrasts for Month			
Mean	1	6.56	0.0137*
Year	1	9.80	0.0030**
Burn	1	1.14	0.2917
Year*Burn	1	1.26	0.2976
Mow	2	2.04	0.1410
Year*Mow	2	1.32	0.2772
Burn*Mow	2	1.70	0.1929
Year*Burn*Mow	2	3.04	0.0573
Quadratic Contrasts for Month			
Mean	1	4.87	0.0323*
Year	1	2.85	0.0982
Burn	1	4.91	0.0316*
Year*Burn	1	2.03	0.1603
Mow	2	1.49	0.2357
Year*Mow	2	4.51	0.0162*
Burn*Mow	2	0.28	0.7558
Year*Burn*Mow	2	2.04	0.1409

Table A38. Repeated measures MANOVA for monthly root biomass from ingrowth cores (log transformed). The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	p
Year	1	47.22	0.0001***
Burn	1	0.12	0.7326
Year*Burn	1	1.38	0.2461
Mow	2	0.57	0.5712
Year*Mow	2	0.11	0.8979
Burn*Mow	2	2.95	0.0635
Year*Burn*Mow	2	2.64	0.0830
Tests of Within Subject Effects			
Month	3	3.73	0.0097**
Month*Year	3	12.95	0.0001***
Month*Burn	3	0.66	0.5712
Month*Year*Burn	3	1.16	0.3268
Month*Mow	6	1.24	0.2922
Month*Year*Mow	6	0.18	0.9790
Month*Burn*Mow	6	0.26	0.9487
Month*Year*Burn*Mow	6	1.32	0.2558
Linear Contrasts for Month			
Mean	1	0.72	0.4013
Year	1	1.72	0.1972
Burn	1	0.76	0.3896
Year*Burn	1	2.26	0.1401
Mow	2	2.61	0.0854
Year*Mow	2	0.16	0.8493
Burn*Mow	2	0.14	0.8716
Year*Burn*Mow	2	0.34	0.7156
Quadratic Contrasts for Month			
Mean	1	11.16	0.0018**
Year	1	2.99	0.0909
Burn	1	0.70	0.4064
Year*Burn	1	0.17	0.6841
Mow	2	0.14	0.8698
Year*Mow	2	0.04	0.9604
Burn*Mow	2	0.51	0.6046
Year*Burn*Mow	2	1.23	0.3020

Table A39. Repeated measures MANOVA for root length density (square root transformed) from ingrowth cores (1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Burn	2	0.60	0.5650
Tests of Within Subject Effects			
Month	3	1.14	0.3441
Month*Burn	6	0.77	0.5755
Linear Contrasts for Month			
Mean	1	0.01	0.9094
Burn	2	0.22	0.8054
Quadratic Contrasts for Month			
Mean	1	4.28	0.0628
Burn	2	1.16	0.3500

Table A40. Repeated measures MANOVA for root biomass production (log transformed) from ingrowth cores (1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Burn	2	1.10	0.3733
Tests of Within Subject Effects			
Month	3	8.52	0.0012**
Month*Burn	6	0.20	0.9534
Linear Contrasts for Month			
Mean	1	11.31	0.0083**
Burn	2	0.31	0.9466
Quadratic Contrasts for Month			
Mean	1	3.92	0.0789
Burn	2	0.09	0.9123

Table A41. Repeated measures MANOVA for mean daily soil temperature (0-10cm). The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Year	1	104.89	0.0001***
Burn	1	2.44	0.1270
Year*Burn	1	0.32	0.5742
Mow	2	0.23	0.7945
Year*Mow	2	0.67	0.5191
Burn*Mow	2	2.18	0.1279
Year*Burn*Mow	2	2.63	0.0865
Tests of Within Subject Effects			
Month	5	174.68	0.0001***
Month*Year	5	102.37	0.0001***
Month*Burn	5	0.63	0.6231
Month*Year*Burn	5	0.44	0.7574
Month*Mow	10	0.58	0.7683
Month*Year*Mow	10	0.99	0.4386
Month*Burn*Mow	10	1.36	0.2303
Month*Year*Burn*Mow	10	1.22	0.2962
Linear Contrasts for Month			
Mean	1	1226.12	0.0001***
Year	1	750.76	0.0001***
Burn	1	3.68	0.0633
Year*Burn	1	0.54	0.4669
Mow	2	1.44	0.2513
Year*Mow	2	0.29	0.7484
Burn*Mow	2	2.19	0.1265
Year*Burn*Mow	2	3.07	0.0593
Quadratic Contrasts for Month			
Mean	1	36.62	0.0001***
Year	1	7.18	0.0112*
Burn	1	0.04	0.8436
Year*Burn	1	0.26	0.6160
Mow	2	0.35	0.7061
Year*Mow	2	0.36	0.6969
Burn*Mow	2	1.95	0.1578
Year*Burn*Mow	2	2.09	0.1385

Table A42. Repeated measures MANOVA for volumetric soil moisture (arcsine transformed; 0-30cm). The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Year	1	43.20	0.0001***
Burn	1	1.33	0.2548
Year*Burn	1	0.08	0.7733
Mow	2	0.49	0.6188
Year*Mow	2	0.85	0.4355
Burn*Mow	2	0.16	0.8527
Year*Burn*Mow	2	1.10	0.3414
Tests of Within Subject Effects			
Month	3	210.24	0.0001***
Month*Year	3	41.51	0.0001***
Month*Burn	3	1.46	0.2257
Month*Year*Burn	3	2.97	0.0324*
Month*Mow	6	0.79	0.5835
Month*Year*Mow	6	0.83	0.5496
Month*Burn*Mow	6	1.51	0.1751
Month*Year*Burn*Mow	6	0.8	0.5795
Linear Contrasts for Month			
Mean	1	422.55	0.0001***
Year	1	73.97	0.0001***
Burn	1	0.59	0.4457
Year*Burn	1	0.17	0.6841
Mow	2	0.22	0.8070
Year*Mow	2	0.86	0.4309
Burn*Mow	2	0.32	0.7293
Year*Burn*Mow	2	0.98	0.3830
Quadratic Contrasts for Month			
Mean	1	1.67	0.2033
Year	1	11.92	0.0012**
Burn	1	0.54	0.4661
Year*Burn	1	4.34	0.0430*
Mow	2	0.16	0.8491
Year*Mow	2	0.57	0.5707
Burn*Mow	2	1.40	0.2563
Year*Burn*Mow	2	0.32	0.7265

Table A43. Repeated measures MANOVA for mean daily soil temperature (0-10cm; 1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Burn	2	1.49	0.2537
Tests of Within Subject Effects			
Month	4	51.20	0.0001***
Month*Burn	8	2.35	0.0980
Linear Contrasts for Month			
Mean	1	61.22	0.0001***
Burn	2	2.69	0.0967
Quadratic Contrasts for Month			
Mean	1	12.17	0.0028**
Burn	2	2.19	0.1420

Table A44. Repeated measures MANOVA for volumetric soil moisture (arcsine transformed; 0-30cm; 1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Burn	2	0.47	0.6328
Tests of Within Subject Effects			
Month	5	42.86	0.0001***
Month*Burn	10	1.55	0.2060
Linear Contrasts for Month			
Mean	1	52.42	0.0001***
Burn	2	0.32	0.7329
Quadratic Contrasts for Month			
Mean	1	0.17	0.6843
Burn	2	0.14	0.8684

Table A45. Repeated measures MANOVA for soil organic carbon (%) from soils collected in August of 1998, 1999. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Depth = soil depth (0-10 cm, 10-20 cm). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Year	1	3.04	0.0896
Burn	1	0.11	0.7397
Year*Burn	1	0.56	0.4608
Mow	2	0.18	0.8395
Year*Mow	2	0.65	0.5275
Burn*Mow	2	0.55	0.5796
Year*Burn*Mow	2	0.09	0.9114
Tests of Within Subject Effects			
Depth	1	17.13	0.0002***
Depth*Year	1	1.08	0.3060
Depth*Burn	1	0.00	0.9834
Depth*Year*Burn	1	0.19	0.6635
Depth*Mow	2	0.07	0.9320
Depth*Year*Mow	2	0.88	0.4217
Depth*Burn*Mow	2	0.43	0.6552
Depth*Year*Burn*Mow	2	1.99	0.1511

Table A46. Repeated measures MANOVA for soil organic carbon from soils collected in August 1999. The two factors are: Burn = prescribed fire (warm season, cool season, control), Depth = soil depth (0-10 cm, 10-20 cm). Because the addition of warm season plots unbalanced the design, only samples from unmown plots were used in the analysis. Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

Source	DF	F value	P
Burn	2	0.16	0.8529
Tests of Within Subject Effects			
Depth	1	9.51	0.0095*
Depth*Burn	2	0.36	0.7050

Table A47. Repeated measures MANOVA for total nitrogen (%) from soils collected in August of 1998, 1999. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Depth = soil depth (0-10 cm, 10-20 cm). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Year	1	1.44	0.2379
Burn	1	0.35	0.5566
Year*Burn	1	1.68	0.2038
Mow	2	0.47	0.6265
Year*Mow	2	0.68	0.5148
Burn*Mow	2	0.16	0.8567
Year*Burn*Mow	2	0.44	0.6472
Tests of Within Subject Effects			
Depth	1	1.17	0.2876
Depth*Year	1	0.54	0.4686
Depth*Burn	1	0.51	0.4811
Depth*Year*Burn	1	0.42	0.5187
Depth*Mow	2	0.47	0.6283
Depth*Year*Mow	2	0.25	0.7821
Depth*Burn*Mow	2	0.38	0.6856
Depth*Year*Burn*Mow	2	0.35	0.7079

Table A48. Repeated measures MANOVA for total nitrogen from soils collected in August 1999. The two factors are: Burn = prescribed fire (warm season, cool season, control), Depth = soil depth (0-10 cm, 10-20 cm). Because the addition of warm season plots unbalanced the design, only samples from unmown plots were used in the analysis. Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

Source	DF	F value	P
Burn	2	0.82	0.4670
Tests of Within Subject Effects			
Depth	1	0.04	0.8422
Depth*Burn	2	0.64	0.5449

Table A49. Repeated measures MANOVA for C:N of soils collected in August of 1998, 1999. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Depth = soil depth (0-10 cm, 10-20 cm). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Year	1	1.30	0.2611
Burn	1	0.23	0.6337
Year*Burn	1	0.64	0.4284
Mow	2	0.38	0.6858
Year*Mow	2	0.65	0.5293
Burn*Mow	2	0.46	0.6359
Year*Burn*Mow	2	0.68	0.5128
Tests of Within Subject Effects			
Depth	1	0.01	0.9192
Depth*Year	1	0.78	0.4005
Depth*Burn	1	0.18	0.6711
Depth*Year*Burn	1	0.51	0.4791
Depth*Mow	2	0.48	0.6213
Depth*Year*Mow	2	0.57	0.5697
Depth*Burn*Mow	2	0.60	0.5527
Depth*Year*Burn*Mow	2	1.45	0.2481

Table A50. Repeated measures MANOVA for C:N of soils collected in August 1999. The two factors are: Burn = prescribed fire (warm season, cool season, control), Depth = soil depth (0-10 cm, 10-20 cm). Because the addition of warm season plots unbalanced the design, only samples from unmown plots were used in the analysis. Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

Source	DF	F value	P
Burn	2	1.29	0.3149
Tests of Within Subject Effects			
Depth	1	2.48	0.1438
Depth*Burn	2	1.23	0.3291

Table A51. Repeated measures MANOVA for soil respiration. The four factors are: Year = year of treatment (1998, 1999), Burn = cool season prescribed fire (burn, control), Mow = simulated grazing treatment (repeatedly mown, once mown, control), Month = month sample collected (March, April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Year	1	230.64	0.0001***
Burn	1	3.04	0.0879
Year*Burn	1	1.50	0.2268
Mow	2	2.67	0.0799
Year*Mow	2	2.86	0.0677
Burn*Mow	2	0.46	0.6348
Year*Burn*Mow	2	0.06	0.9414
Tests of Within Subject Effects			
Month	5	61.54	0.0001***
Month*Year	5	44.46	0.0001***
Month*Burn	5	3.41	0.0101*
Month*Year*Burn	5	0.58	0.6785
Month*Mow	10	1.68	0.1046
Month*Year*Mow	10	0.94	0.4888
Month*Burn*Mow	10	0.99	0.4489
Month*Year*Burn*Mow	10	0.61	0.7717
Linear Contrasts for Month			
Mean	1	131.68	0.0001***
Year	1	269.27	0.0001***
Burn	1	2.63	0.1120
Year*Burn	1	0.04	0.8388
Mow	2	0.99	0.3788
Year*Mow	2	3.02	0.0586
Burn*Mow	2	1.02	0.3680
Year*Burn*Mow	2	2.42	0.1006
Quadratic Contrasts for Month			
Mean	1	53.10	0.0001***
Year	1	0.01	0.9422
Burn	1	2.71	0.1066
Year*Burn	1	0.37	0.5485
Mow	2	1.87	0.1653
Year*Mow	2	0.13	0.8770
Burn*Mow	2	0.43	0.6549
Year*Burn*Mow	2	0.65	0.5284

Table A52. Repeated measures MANOVA for monthly soil respiration (1999 only). The factors are: Burn = prescribed fire (warm season, cool season, control), and Month = month sample collected (April, May, June, July, August). Significant differences are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$). For within subject effects, Greenhouse-Geisser adjustment was used to correct for autocorrelation among repeated measure factor Month. Significance levels for polynomial contrasts are modified by Bonferroni adjustment.

Source	DF	F value	P
Burn	2	1.92	0.1889
Tests of Within Subject Effects			
Month	5	40.05	0.0001***
Month*Burn	10	1.48	0.2019
Linear Contrasts for Month			
Mean	1	175.00	0.0001***
Burn	2	2.35	0.1381
Quadratic Contrasts for Month			
Mean	1	38.69	0.0001***
Burn	2	2.72	0.1063

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